

Oceanic atoll provides refuge for elasmobranchs amidst global declines and promotes opportunities to finance conservation

by

Kaitlyn Zerr
B.Sc., Dalhousie University, 2018

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We acknowledge and respect the Lək̓ʷəŋən (Songhees and Esquimalt) Peoples on whose territory the university stands, and the Lək̓ʷəŋən and W̱SÁNEĆ Peoples whose historical relationships with the land continue to this day.

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Abstract

Sharks and rays (elasmobranchs) are charismatic megafauna that support healthy ecosystems and can serve as flagship species for marine conservation. Elasmobranchs tend to be highly mobile, mid- to high trophic level predators, with slow population growth rates that render them vulnerable to overexploitation. While many species have experienced widespread and ongoing population declines, some nations have recognized the value of elasmobranchs to the tourism industry. The Republic of Maldives has protected sharks and rays from exploitation within their national waters since 2014 because of the significant amount of revenue lost from the tourism industry when populations there began to show signs of overexploitation. However, local threats such as bycatch, entanglement in fishing gear, and unregulated tourism may continue to negatively impact populations, highlighting the need for additional conservation measures. Known as ‘Shark Island’, Fuvahmulah Atoll, a recently designated UNESCO Biosphere Reserve, has recently experienced a steep rise in dive tourism due to improved accessibility to, and awareness of, its abundant and diverse shark and ray megafauna. Although a marine protected area (MPA) has been designated at the southern end of the atoll, a management plan has not yet been developed and species-specific information is lacking. Furthermore, it is unclear if dive tourists are willing to contribute financially to help conserve the biodiversity upon which their tourism depends. Here, we sought to inform management plans and policy design by 1) quantifying elasmobranch assemblages on Fuvahmulah Atoll’s reefs and 2) examining tourists’ willingness to pay for increased conservation action on the atoll. In Chapter 2, we deployed remote timelapse cameras at three shallow fore reef sites and collected images on 63 days over a 6-month period. From a total of 1,629,756 images, we calculated the occurrence and relative abundance within days and hours to assess spatial and temporal variations in

elasmobranch visitation to the sites. Sharks and rays were captured on 72% of hours and 95% of days, with the highest number of occurrences recorded at the site within an MPA, Farikedede, followed by Kedevari and Hudhekede. Both reef sharks and apex sharks were represented, with whitetip reef sharks, pelagic threshers, grey reef sharks, tiger sharks, and silvertip sharks, representing the most frequently observed species. We show that Farikedede MPA is a hotspot for reef sharks and tiger sharks. However, Kedevari appears to be an ecologically significant site for pelagic threshers. In Chapter 3, we conducted stated preference surveys with tourists visiting Fuvahmulah to assess tourists' willingness to pay a one-time "Reserve" entrance fee, the factors that influence the value of the fee, and their preferences for conservation measures proposed by the community. Virtually all (97%) tourists were supportive of paying a one-time reserve entrance fee, with an average fee of US\$58 per person. Tourists with more positive environmental attitudes, those more committed to dive tourism (higher skill levels and more frequent trips), and those who encountered specific shark species (tiger sharks or pelagic threshers) in Fuvahmulah were willing to pay higher entrance fees. Visitors to Fuvahmulah Atoll highly value marine conservation, and their financial support creates unique opportunities to safeguard biodiversity and ensure the sustainability of the tourism industry. Increasing our understanding of the biological community while exploring avenues to finance conservation can provide opportunities to create informed and comprehensive management plans. While many elasmobranch populations continue to experience global declines, protected and well-managed sites may increase resilience on a global scale.

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Dedication

Fuvahmulakige ravvehsunna

To those who call Fuvahmulah Atoll home

Chapter 1 – Introduction

Sharks and rays are charismatic megafauna that support healthy ecosystems and can serve as flagship species for ocean conservation. These cartilaginous fishes, which belong to the subclass Elasmobranchii of the Class Chondrichthyes, tend to be highly mobile, mid- to high trophic level predators, with slow population growth rates that render them vulnerable to overexploitation (Musick et al., 2000; Roff et al., 2016; Shipley et al., 2023). Indeed, global declines of elasmobranchs have been largely attributed to the rapid expansion of fisheries operating in the open ocean from the 1960s onward (Bonfil, 1994; Rose, 1996; Baum et al., 2003; Baum & Myers, 2004; Nadon et al., 2012; MacNeil et al., 2020a; Dulvy et al., 2021; Pacoureau et al., 2021; Simpfendorfer et al., 2023). In countries around the world and on the high seas, elasmobranchs are landed in both targeted and bycatch fisheries for the high value of their fins or gill plates (Rose, 1996; McClenachan et al., 2016; O'Malley et al., 2017). Initially, research reported the decline of oceanic species, which have been greatly affected by offshore longline fisheries (Baum et al., 2003; Baum & Myers, 2004). Declines in the open ocean have reached 99% for some species; however, declines in reef shark species, which were previously thought to be less impacted by fisheries, have also been documented, with common reef-associated species declining by up to 73% (Baum & Myers, 2004; Simpfendorfer et al., 2023). Diver surveys have revealed that declines of reef-associated elasmobranch species mirror those of pelagic species, with the most severe impacts occurring on reefs near areas of high human density (Graham et al., 2010; Ward-Paige et al., 2010; Nadon et al., 2012). Recent studies estimate that more than half of reef-associated sharks and rays are threatened with extinction (Sherman et al., 2023). Furthermore, MacNeil et al. (2020) report a complete absence of reef

sharks from 20% of coral reefs worldwide. The growing concern for elasmobranch population declines has led to international interest in conservation strategies.

1.1 Management and conservation measures for elasmobranchs

Although marine protected areas (MPAs) are often promoted as a strategy for elasmobranch conservation, the efficacy of these spatial protections for highly mobile species like elasmobranchs remains highly debated (Robbins et al., 2006; MacKeracher et al., 2019; Dwyer et al., 2020). Positive impacts of MPA designation have been documented for some reef shark species (McCook et al., 2010; Bond et al., 2012; Goetze & Fullwood, 2013; Flowers et al., 2022; Goetze et al., 2024). A recent study analyzing protected areas on coral reefs worldwide demonstrates that shark populations within MPAs are highest when associated with regions with less historical shark fishing, have specific fisheries regulations, and are well enforced (Goetze et al., 2024). While area-based management may be an effective strategy for reef-associated species with small home ranges, we often lack the knowledge required to design effective MPAs for elasmobranchs (Dwyer et al., 2020). Furthermore, conservation strategies for wide-ranging species, which may be making transboundary movements, are more complex yet critical, considering wide-ranging species face an elevated risk of extinction (Dwyer et al., 2020; Flowers et al., 2022; Sherman et al., 2023). For species which may not remain within the confines of a single MPA, networks which may protect multiple habitat types and fisheries management at the national level are suggested as more effective conservation strategies (Graham et al., 2016; Goetze et al., 2024). Studies investigating the efficacy of shark sanctuaries, which protect species from exploitation within national waters, reveal that these designations are likely not enough in isolation (Ward-Paige, 2017; Ward-Paige & Worm, 2017). Local threats, such as bycatch, entanglement, or unregulated tourism, may continue to impact elasmobranch populations

(Venables et al., 2016; Ward-Paige & Worm, 2017; Murray et al., 2020; Legaspi et al., 2020). Therefore, shark and ray populations may benefit from national protection coupled with area-based management.

A common barrier to MPA success is the long-term financing required to support management and enforcement, critical components of effective MPAs. (Bohorquez et al., 2019; Brown et al., 2023). The economic gain from tourism has motivated some countries to grant national protection to sharks and rays, and the revenue gained can provide opportunities for conservation financing (Depondt & Green, 2006; Terk & Knowlton, 2010; Brown et al., 2023). Interest in shark diving, for example, has increased substantially on a global scale, and visitor fees may be a viable option to help finance conservation, considering charismatic megafauna has been shown to positively affect tourist donation behaviour (Walpole & Leader-Williams, 2002; Kontoleon & Swanson, 2003; Cisneros-Montemayor et al., 2013; Colléony et al., 2017; Zimmerhackel et al., 2019). Indeed, dive tourists tend to show concern for marine ecosystems and wildlife and are generally willing to pay park entrance fees to support conservation in protected areas (Peters & Hawkins, 2009; Grafeld et al., 2016). The value charged by protected areas has been determined using many methods ranging from policymakers' intuition to carefully designed empirical research (Peters & Hawkins, 2009).

Contingent valuation is a stated preference method that uses questionnaires to assess people's willingness to pay for a change in an environmental good (Johnston et al., 2017). Using this method, respondents are presented with a baseline scenario and a proposed change and are asked to state how much they would be willing to pay for the proposed change. Although the literature has highlighted concerns regarding the potential hypothetical bias present in responses, guidelines for survey design were outlined by the National Oceanic and Atmospheric Association

(Arrow et al., 1993), and later updated by Johnston et al. (2017), to increase validity and minimize bias. Contingent valuation methods have been used widely for environmental valuation research. Results have been used as central components for resource damage assessments, decision making, advocacy, and policy design (Johnston et al., 2017). When uncertainties surround the potential impact on the tourism industry, this method can directly assess the willingness of tourists to contribute to conservation through entrance fees and determine an appropriate level of payment (Walpole et al., 2001; Tisdell & Wilson, 2002; Peters & Hawkins, 2009).

1.2 Study location

The Republic of Maldives, situated in the Indian Ocean, has offered national protection to sharks and rays since 2014 (Government of the Maldives President's Office, 2010; EPA, 2014; Ali & Sinan, 2015). Currently, tourism is the island nation's largest industry (Zimmerhackel et al., 2019). Additionally, the tourism levels are dependent on healthy elasmobranch populations (Anderson et al., 2011b; Cagua et al., 2014; Ministry of Tourism, 2022). Shark fishing occurring in the 1990s led to a noticeable decline in species encounters at dive sites, and as a result, the tourism industry suffered significant losses (Anderson et al., 1999; Anderson & Ahmed, 1993; Ali & Sinan, 2014). In response to these economic losses, the Maldives exclusive economic zone (more than 900,000km²) was declared a shark sanctuary in 2010, protecting shark species from catch, captivity, trade, and harm (Government of the Maldives President's Office, 2010; Ali & Sinan, 2014; Ward-Paige, 2017). Ray species were secondarily afforded protection in 2014 (EPA, 2014). Marine megafauna encounters remain an important component of tourism to the Maldives and snorkelling and diving are among the most popular activities of guests (Zimmerhackel et al., 2018; Ministry of Tourism, 2022). Recent estimates suggest that shark and

manta ray diving contribute US\$8.1 million and US\$14.4 million per year in direct revenue, respectively, offering considerable support to the country's economic growth (Anderson et al., 2011; Zimmerhackel et al., 2019). Protective efforts are in place for some sites which provide tourist opportunities to encounter megafauna (MCCEE, 2024). However, very few MPAs within the country have strong management plans in place. Currently, the Maldives' Ministry of Climate Change, Environment, and Energy is working towards developing effective management plans for existing MPAs and identifying additional areas of ecological significance as candidates for increased protection (MCCEE, 2024).

This thesis research took place on Fuvahmulah (Gnaviyani) Atoll, an isolated single-island atoll located in the southernmost region of the Maldives. Fuvahmulah has recently experienced a steep rise in dive tourism due to increased access to this area and an increased awareness of the diverse and abundant elasmobranch megafauna found here (Araujo et al., 2024). The atoll was designated a UNESCO Biosphere Reserve in 2020 in recognition of the significant biodiversity in Fuvahmulah's marine and terrestrial ecosystems (UNESCO, 2020). Fuvahmulah's protected areas include two mangrove ecosystems, Bandaara Kilhi and Dhandimagu Kilhi, and their surrounding wetland ecosystems, which support diverse flora and fauna communities (MCCEE, 2024). A third protected area known as "Thundi Area" is considered both marine and terrestrial and is located on the island's northeast corner. The sand pit of the Thundi Area is dynamic and changes as currents around Fuvahmulah shift. Protection efforts aim to control the amount of sand removed at this site for construction (MCCEE, 2024). One MPA, Farikede, has been recently designated on the southern edge of the reef to increase marine ecosystem protection (MCCEE, 2024). Management plans for the UNESCO Biosphere Reserve and Farikede MPA are still being developed. However, studies have not yet been

conducted to identify the elasmobranch diversity within the MPA and on Fuvahmulah's reefs in general. Furthermore, tourists are increasingly visiting Fuvahmulah, and the community remains divided about the potential negative impacts of visitor fees on the tourism industry.

1.3 Thesis research

This thesis aims to quantify the elasmobranch assemblage of a remote Indian Ocean atoll and assess the potential contribution of tourism to the conservation of these shark and ray species. Specifically, my collaborators and I (1) recorded the diversity and visitation rates of different elasmobranch species in Fuvahmulah Atoll and investigated how they changed spatially (across the atoll) and temporally (diurnally and seasonally), and (2) conducted surveys with visiting tourists assessing their willingness to pay (WTP) to support conservation initiatives and the factors that influence tourists' WTP.

In Chapter 2, we investigate the identity and visitation patterns of megafauna in the region by monitoring three fore reef sites with unbaited timelapse cameras. Fuvahmulah Dive School guides and staff deployed cameras; images were captured every 2 seconds over six months. In total, 63 days of recorded images were collected and analyzed. Overall, four ray species and seven shark species were observed, the most common of which were whitetip reef shark, pelagic thresher, and grey reef shark, observed on 89%, 83% and 78% of days, respectively. We demonstrate that Farikede's MPA is a hotspot for reef-associated sharks and tiger sharks. Additionally, we recorded consistent occurrence of pelagic thresher sharks throughout the study period and highlighted the importance of a site beyond the MPA for this species. By analyzing the spatial and temporal trends of the elasmobranch occurrence and relative abundance over hours and days, we contribute species-specific knowledge to developing MPA management plans and suggest directions for future research.

In Chapter 3, we empirically evaluate the willingness of tourists to financially contribute to conservation initiatives at Fuvahmulah Atoll through Biosphere Reserve entrance fees. We demonstrate that Fuvahmulah Atoll attracts committed and environmentally conscious scuba divers, and nearly all visitors are willing to contribute financially to support conservation initiatives. Tourist preferences reveal that MPA management and waste management receive more support than community education and marine research facilities. Additionally, we provide evidence that encounters with specific shark species, namely pelagic thresher or tiger sharks, motivate visitation and promote higher WTP values. Our results suggest that tourism can support increased conservation measures, and that the sustainability of the tourism industry depends upon effective shark conservation.

Together, this research provides novel insights into how Fuvahmulah Atoll is a refuge for shark species experiencing global population declines and attracts dive tourists who are willing to contribute to conservation. Our work contributes to the growing knowledge of the importance of remote locations for elasmobranch species and how a rising dependence on tourism can, and should, be accompanied by an increased capacity for environmental protection. In the face of a biodiversity crisis caused by human impacts, there is an urgent need to identify locations which act as refuge for species facing global population declines. Protecting these sites provides resilience to the coastal communities depending on them and is a critical step for regional and global conservation efforts.

Chapter 2 - Oceanic atoll in South of Maldives offers refuge for species amidst global declines

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2.1 Abstract

Sharks and rays (elasmobranchs) support both marine ecosystem function and the livelihoods of people on island nations through tourism. However, both oceanic and reef-associated elasmobranchs have experienced widespread declines globally. Within the Indian Ocean, Fuvahmulah Atoll, a highly exposed oceanic atoll in the south of the Republic of Maldives, is increasingly recognized for its abundant elasmobranch megafauna. Yet despite a recent UNESCO Biosphere Reserve designation, Fuvahmulah's elasmobranch populations are not well studied. Using remote timelapse cameras at three shallow fore reef sites on the atoll, we quantified elasmobranch visitations during daylight hours over a six-month period (March – August) in 2022. Overall, four ray species and seven shark species were observed, the most common of which were the whitetip reef shark, pelagic thresher, and grey reef shark which were observed on 89%, 83% and 78% of days, respectively. Community composition at the sites was similar but more consistent over days at Farikede. The daily activity (relative abundance, and FO; # of hours obs/total hours recorded) of tiger sharks and thresher sharks declined throughout the study period. However, we found no impact of date on pelagic thresher occurrence while the occurrence of tiger sharks declined over days. In contrast, the daily relative abundance and FO (# hours obs/total hours recorded) of reef sharks increased throughout the study. Species-specific diurnal patterns were also observed. Overall, the most sightings occurred within the island's only marine protected area, Farikede. Furthermore, occurrence (daily and hourly), relative abundance (daily MaxN) and FO (# hours obs/total hours recorded) of tiger sharks and reef sharks was highest at Farikede. These findings represent the first quantitative descriptions of Fuvahmulah Atoll's elasmobranch community and highlight the atoll as an important site for sharks and rays.

While many species continue to experience global declines, protected and well managed sites may increase resilience on a global scale.

2.2 Introduction

Elasmobranchs maintain diverse roles within marine ecosystems and have significant influence on predator prey dynamics and the movement of nutrients across trophic levels (Baum & Worm, 2009; Simpfendorfer et al., 2023). However, following significant increases in direct and indirect fishing pressure, the global abundance of oceanic sharks and rays is estimated to have declined by over 70% in the past four decades (Baum et al., 2003; Baum & Myers, 2004; Pacoureau et al., 2021). Recent studies indicate that reef sharks, which had previously been considered less threatened by the International Union for the Conservation of Nature (IUCN), have also declined substantially on a global scale (MacNeil et al., 2020a; Nadon et al., 2012; Osgood & Baum, 2015; Simpfendorfer et al., 2023). In addition to fisheries impacts, climate change and habitat degradation compound the risk of elasmobranch extinction (Dulvy et al., 2021; Hyde et al., 2022; Jorgensen et al., 2022), with important implications for the coastal communities depending on ocean resources (Simpfendorfer et al. 2023; Jorgensen et al. 2022).

Amidst intense global fishing pressure, highly protected areas with the capacity for monitoring and enforcement are increasingly important for ensuring elasmobranch population persistence (Simpfendorfer et al., 2023; Jorgensen et al., 2022). Identifying areas of importance for shark and ray populations and developing species-specific management plans has thus emerged as a conservation and research priority (Hyde et al., 2022; Jorgensen et al., 2022; Simpfendorfer et al., 2023). In particular, remote oceanic islands and atolls may provide a refuge for threatened shark and ray species (Stevenson et al., 2007; Nadon et al., 2012; Nalesso et al., 2019). Oceanic islands generate habitat complexity in the open ocean and create biodiversity

hotspots supporting both oceanic and reef-associated elasmobranchs (Worm et al., 2003; Nalesso et al., 2019; Mazzei et al., 2021). Beyond the ecosystem functions gained by healthy elasmobranch populations, sharks and rays also provide opportunities for economic growth for the coastal communities in these regions through dive related tourism (Cisneros-Montemayor et al., 2013; O'Malley et al., 2013). Income generated by the tourism industry therefore provides additional incentive for ensuring shark and ray populations are adequately protected from population declines (Cisneros-Montemayor et al., 2013; O'Malley et al., 2013).

In the Indian Ocean, tourism, which generates employment and supports livelihoods, is the main economic driver of the Republic of Maldives (Zimmerhackel et al., 2019). With snorkelling and diving rated the most popular activities among tourists visiting the island nation, the tourism industry depends upon on the persistence of shark and ray populations (Anderson, et al., 2011b; Cagua et al., 2014; Ministry of Tourism, 2022). For example, in the 1990's unsustainable shark fishing depleted shark populations and resulted in a decline in tourism and significant losses to the dive tourism industry (Anderson & Ahmed, 1993; Anderson et al., 1999; Ali & Sinan, 2014). In 2010, the Government of the Maldives responded to tourism losses by declaring the country a shark sanctuary, legally protecting sharks from exploitation (Ali & Sinan, 2015; Government of the Maldives President's Office, 2010). Furthermore, all ray species were given national protection in 2014 (EPA, 2014). As the interest in shark-diving grows on a global scale, the income generated in the Maldives from shark and ray diving has increased substantially (Cisneros-Montemayor et al., 2013; Zimmerhackel et al., 2019). Recent studies estimate that shark and ray diving collectively contribute US\$29.8 million per year in direct revenue in the Maldives (Anderson et al., 2011b; O'Malley et al., 2013; Zimmerhackel et al., 2019). However, tourism, may also put vulnerable species at risk by disturbing the natural

behaviours of sharks and rays, increasing habitat degradation, or causing injury from boat traffic (Hall, 2010; Venables et al., 2016; Murray et al., 2020; Harvey-Carroll et al., 2021).

Although some marine protected areas (MPAs) within the Maldives have strong management plans in place to protect economically important megafauna, the Ministry of Climate Change, Environment and Energy and associated partners are currently working towards identifying additional areas of ecological significance and developing effective management plans for these areas (MCCEE, 2024). Fuvahmulah Atoll, located in the far south, is the country's only single island atoll and is referred to as 'Shark Island'. Fuvahmulah Atoll's unique marine and terrestrial biodiversity is recognized globally through its recent declaration as a UNESCO Biosphere Reserve (UNESCO, 2020). To date, Fuvahmulah has only a single MPA, located at the southern end of the island encompassing an area of 6.4km², which does not yet have an implemented management plan (MCCEE, 2024). Tourist access to this remote region in the Maldives increased with the opening of a domestic airport in 2011 (Araujo et al., 2024). Dive tourists from around the world are increasingly visiting Fuvahmulah Atoll which has become well known for the abundant shark and ray megafauna found here. Currently, more than 10,000 dive tourists visit Fuvahmulah annually (Araujo et al., 2024). An understanding of the species present in Fuvahmulah Atoll, as well as which areas might be of particular ecological importance, is critical to developing management plans that safeguard the shark and ray populations which tourism depends on (García-Barón et al., 2019; Graham et al., 2016).

The vulnerabilities of elasmobranchs to anthropogenic threats, such as unregulated tourism and bycatch, as well as the efficacy of spatial protection, may depend on their habitat use and movement patterns (Graham et al., 2016; Dwyer et al., 2020; Flowers et al., 2022). Both oceanic and reef-associated elasmobranchs have been encountered by divers in Fuvahmulah.

Reef-associated sharks, which typically have small home ranges (2-10km²), show diurnal changes in habitat use, utilizing shallow waters at dawn and dusk, when they may have increased foraging opportunities (Whitney et al., 2007; Vianna et al., 2013; Dwyer et al., 2020; Beauvais et al., 2024). Additionally, reef-associated species tend to prefer habitats that incorporate specific reef features such as high levels of hard coral coverage, benthic complexity, and reef slopes which are exposed to high current flow (Vianna et al., 2013; Espinoza et al., 2014; Lester et al., 2022). In contrast, oceanic species demonstrate transboundary movements to track increases in productivity offshore, to mate, or give birth (Meyer et al., 2009; Holmes et al., 2014; Werry et al., 2014; Lea et al., 2018). Some studies suggest that site fidelity of oceanic species may sex specific or depend on ontogeny (Lea et al., 2018; Polo-Silva et al., 2013; Werry et al., 2014).

To advance understanding of the elasmobranch assemblages occupying Fuvahmulah Atoll's reefs, we monitored three sites from sunrise to sunset using remote timelapse cameras over a six-month period (March to August 2022). Specifically, we aimed to: 1) determine the elasmobranch species present in the area, and 2) quantify the spatial and temporal variation of species sightings. We hypothesized that the occurrence and relative abundance of reef sharks would vary across hours, with increased activity occurring at dusk and dawn. In contrast, we hypothesized that apex predators would be transient at the atoll, with their occurrence and relative abundance increasing, due to oceanographic changes, during the Southwest Monsoon period. Due to the exposed and sloping nature of the southern reef, Farikedu, we further hypothesized that this site would have the most reef shark activity. However, we suspected that transient species would be less site attached than reef sharks. By recording elasmobranch assemblages and visitation patterns, we provide critical knowledge for species specific management actions and recommendations for future research.

2.3 Methods

2.3.1 Study site and design

The Republic of Maldives consists of 26 atolls and extends 870km spanning the equator (Figure 2.1; Stevens & Froman, 2019). Fuvahmulah Atoll ($0^{\circ}17'56.22''\text{S}$, $73^{\circ}25'35.94''\text{E}$) is one of the country's southernmost atolls, located 494km south of the capital, Malé. Tourism to Fuvahmulah has been introduced relatively recently and development has increased with more tourists visiting each year. The first dive centre opened in Fuvahmulah in 2013, and eleven dive centres currently operate on the island with tourism primarily driven by shark diving (Araujo et al., 2024).

To investigate the visitation of elasmobranch species on Fuvahmulah Atoll (Republic of Maldives) reefs, we intensively surveyed 3 fore reef sites, Hudhekede, Kedevari, and Farikede, with remote timelapse cameras from March to August 2022 on 63 days (Figure 2.1). Camera deployment locations were selected based on dive sites to aid in camera deployment and retrieval. Due to rough conditions on the west side during the study period, deployments were restricted to the northern, eastern and southern part of the island.

2.3.2 Camera system

Each camera system setup consisted of two external power banks (Voltaic V75) linked together and connected to a GoPro (Hero 8 model). GoPro Labs firmware was downloaded and installed on each camera (Hero 8 Black model, <https://gopro.github.io/labs/>). Timelapse settings were configured with GoPro Labs QR Code Creator (<https://gopro.github.io/labs/control/custom/>) to switch on at sunrise and off at sunset to preserve memory card space and maximize battery life. The camera, power banks and associated cables

were attached via cable ties to an electronics tray that was then placed inside of a Blue Robotics watertight housing (<https://bluerobotics.com/store/watertight-enclosures/wte-vp/#tube>). Prior to camera deployments, small concrete blocks with metal bar attachments were deployed to mark each site, secure the positively buoyant system setup, and ensure a consistent angle was maintained across deployments. Blocks remained in place throughout the study duration. Based on pilot testing conduct in 2018 with the Manta Trust, Maldives Manta Conservation Programme and Fuvahmulah Dive School, an image capture rate of 1 photo per minute resulted in a 20% decline in identifiable images of megafauna species when compared to a capture rate of 1 photo per 2 second interval. Therefore, in the current study, one system setup was deployed at each site and a capture rate of one image per two seconds was used. System setups were collected every four days (when battery life was depleted) and replaced with a fully charged systems in attempt to minimize data gaps. Systems were secured to the metal bars of the block with a dive weight belt.

2.3.3 Image processing

Metadata (file name, date, time of image) were extracted for all images with the use of an Exif tool and then organized in Microsoft Excel according to site. With approximately 20,000 images captured at each site/day, images were imported into Adobe Premiere Pro (version 23.1.0) and stitched together at a frame rate of 10 frames/second to streamline video processing. Processing accuracy at different playback frame rates, was tested with volunteers of the Manta Trust and the Maldives Whaleshark Programme during data collection in March 2022. Tests revealed that sightings missed by volunteers were minimized when volunteers analyzed footage at a rate of 10 frames per second. When megafauna appeared in the videos, the video was paused and sightings were recorded in an excel spreadsheet describing the date, site, time of image,

species present, and number of individuals. Additionally, for each sighting, a measure of certainty was included on a scale of 1 to 3 (Table A1). Images that were unidentifiable were marked as such and checked by the lead author. Data entered by volunteers was double checked and corrected until corrections were no longer necessary to prevent misidentifications and ensure minimal observed bias.

2.3.4 Statistical analysis

From the image data, we quantified the following metrics for each species at both the daily and hourly level;

- 1) **Occurrence**: defined as a 0 when absent and 1 when present (presence-absence).
- 2) **Relative abundance**: defined as the maximum number of individuals in one frame at any point within an hour or day (MaxN).
- 3) **Frequency of Occurrence**; (FO) defined as the proportion of occurrence within a given timestep. **Sub-daily FO** represents the proportion of hours within a day in which a presence was recorded. **Sub-hourly FO** represents the proportion of ten-minute intervals within an hour in which a presence was recorded. Sub metrics are used as a proxy for the duration of occupancy at a site within a day and hour.

For metrics at the hourly level, hours on different days were considered independent data points.

We evaluated the influence of site and date category (early-mid-late) on elasmobranch community composition via non-metric multidimensional scaling (NMDS) using the package ‘vegan’ v2.4-6 (Okasanen et al., 2022) in R v4.2.2 (R Core Team, 2022). First, we constructed two Bray-Curtis dissimilarity matrices, one of which described the daily occurrence and relative abundance of all species recorded during the study, and a second that described the sub-daily FO of all species recorded. Metadata included site, and date which was categorized as “early”

(March-April), “mid” (May-June) or “late” (July-August) based on roughly even divides of sampling dates. Significant species scores ($p < 0.05$; Table A9) were projected onto each NMDS. Resulting ordinations displayed site, and date category separately for both variables (occurrence/relative abundance and sub-daily FO). Next, we tested for significant differences in community composition through permutational multivariate analysis of variance (PERMANOVA) tests with 999 permutations and Bray-Curtis distances using the *andonis2* function (Okasanen et al., 2022). Site and study period category were used as fixed effects in separate models. *Post hoc* pairwise comparisons were conducted if PERMANOVA results were significant ($p < 0.05$). Finally, to examine differences in the dispersion of sites or date categories, we tested beta dispersion using the *betadisper* function and a subsequent permutation test for homogeneity of multivariate dispersions with 999 permutations (Okasanen et al., 2022).

We then used generalized linear modelling (GLMs) to investigate the influence of site, date and hour on 1) daily and hourly occurrence, 2) daily and hourly relative abundance, and 3) sub-daily and sub-hourly FO of each of the five most frequently sighted species: whitetip reef sharks (*Triaenodon obesus*), pelagic threshers (*Alopias pelagicus*), grey reef sharks (*Carcharhinus amblyrhynchos*), tiger sharks (*Galeocerdo cuvier*), and silvertip sharks (*Carcharhinus albimarginatus*). The remainder of the observed species, which were observed on less than 5% of hours recorded, were left out of the analysis due to low sightings in the dataset (Table 2.1). Separate GLMs were built to investigate changes over days and hours and the daily and hourly metrics were used as response variables where appropriate. Considering relative abundance may be governed by a separate process by which a presence-absence occurs, we modeled occurrence data and relative abundance data together using a hurdle modelling approach where possible using the *hurdle* function from the package ‘pscl’ v1.5.5.1 (Zeileis et

al., 2008). In this two-step process, a binomial probability model is first used to determine whether a zero or non-zero outcome occurs and a second step fits a separate model for positive outcomes using a Poisson or negative binomial distribution. Modeling the positive outcomes based on truncated data allows us to answer questions about relative abundance when a presence is determined ie. when the species is present, in what abundance. Occurrence and relative abundance trends across days and hours were analyzed using the hurdle model approach with the exception of daily occurrence trends of grey reef sharks and tiger sharks which were present within each day recorded at Farikede. Occurrence models for these species therefore had complete separation with 100% success at Farikede and required bias-reduced logistic regression from the R package *brglm2* (Kosmidis & Pagui, 2023). Count models were run separately in this case and included absences. Proportional data (sub-daily and sub-hourly FO) was modeled using the quasibinomial distributions. For models examining the occurrence and relative abundance as separate processes, as well as for all FO models, the *glm* function from the ‘stats’ package was used (R Core Team, 2022).

For all three metrics (occurrence, relative abundance, FO), site, date, and the interaction between them were included as fixed effects in the models to investigate trends over days. Site, and hour, as well as the interaction between them, were included as fixed effects to investigate trends over hours. To account for varying recording durations across deployments, “effort”, measured by the number of images captured within each day or hour, was included as an offset term for all occurrence and relative abundance models. Similarly, the number of 1 hour and 10-minute intervals was included as weights argument for the sub-daily and sub-hourly FO models. Normality assumptions and homogeneity of variance were evaluated for each model, and for each case appeared reasonable. Best-fit models were selected based on the lowest AICc (Akaike

information criterion with a correction for small sample sizes) or the model which captured the most significant terms that was within dAICc of 2.0 of the best fit model. Interactions that were non-significant were removed from the best-fit model. Hour was modeled as a quadratic (second-order) polynomial to allow for the fact that sightings of species would likely peak at some point during the day. If the second-order polynomial of the hour term was non-significant in the best-fit model, it was removed, and no transformation of hour was defined. Planned contrasts were conducted for *post hoc* analysis on differences between the three sites or site-hour interactions for each best-fit model using the functions *emmeans* and *contrast* from the package ‘emmeans’ v1.10.1 (Lenth, 2024). Top models, as well as estimates and p-values are included in **Appendix A** (Table A2-A6).

2.3.5 Data availability

The data and R code used in the statistical analysis for this study will be made publicly available through GitHub (<https://github.com/baumlab>) upon manuscript acceptance.

2.4 Results

Overall, 4 species of ray, 7 species of shark and 1 species of turtle were captured by the timelapse cameras (Table 2.1), with at least one elasmobranch captured on 72% of hours and 95% of days (n = 550/743 hours; n = 60/63 days). The highest number of elasmobranch occurrences were recorded at Farikedede (90.73% hours), followed by Kedeveri (66.74% hours) and Hudhekede (46.62% hours; Table A7). Although the pelagic thresher shark was observed in the most images overall (n = 27,447, 1.6%), which accounted for over half of all identifications (54.15%; Figure A1), whitetip reef sharks were observed on the most days and within the most hours (Table 2.1, Figure 2.2a, Figure A2a). This difference reflects the long durations of pelagic

thresher shark presence at Kedevari (Figure A1a,c). After whitetip reef sharks, pelagic thresher sharks followed by grey reef sharks were observed on the most days and hours (Table 2.1, Figure A2, Figure 2.2a). At Farikede, most identifications were of grey reef sharks, followed by pelagic threshers and whitetip reef sharks (Figure A1d), while whitetip reef sharks dominated sightings at Hudhekede, (Figure A1b).

2.4.1 Community composition

Overall, megafauna community composition varied significantly across the sites (permanova $p = 0.001$; Table 2.2, Figure 2.3, Table A8). However, the sites shared the occurrence and relative abundance of many species. The occurrence and relative abundance of oceanic manta rays, hawksbill sea turtles, tiger sharks, and pelagic threshers was more associated with Hudhekede and Kedevari (Figure 2.3, Table A8). Although not significant when examining community composition based on occurrence and relative abundance, a trend of declining dispersion was identified on a gradient from North to South likely reflecting more consistent sightings at Farikede (Table 2.3; Figure 2.3). Site differences were stronger when examining community composition based on the sub-daily FO (# of hours with observations in a day/total hours sampled in a day) of species where sharks were highly associated with Farikede (and to a lesser extent, Kedevari) reflecting higher amounts of time spent at this site (Figure 2.3b, Table A8). Pelagic threshers were additionally associated with Kedevari (Figure 2.3b).

In addition to site differences, megafauna community composition significantly changed throughout the study period (permanova $p = 0.001$; Figure 2.4, Table 2.2, Table A8). The occurrence and relative abundance of oceanic manta rays, hawksbill sea turtles and tiger sharks were more associated with sampling days early and mid-study period and community composition homogenized throughout toward the later portion of the study period (Figure 2.4a,

Table 2.3, Table A8). Shifts across days also occurred within the sub-daily FO of communities wherein higher proportions of the day in which tiger sharks, grey reef sharks and silvertips were recorded was increasingly associated with later portions of the study period (Figure 2.4b). The association of pelagic threshers, scalloped hammerheads and whitetip reef sharks likely reflected site level differences (Figure 2.3b, Figure 2.4b).

2.4.2 Whitetip reef shark *Triaenodon obesus*

Daily relative abundance was highest at Farikedede relative to the other sites and increased throughout the study period (Figure 2.6b, Table A5). Hourly whitetip reef shark occurrence and relative abundance was higher at Hudhekede and Farikedede relative to Kedevari, however occurrence and relative abundance significantly declined across hours at Hudhekede (Figure 2.6c,d, Table A4, Table A5). Sub-hourly FO declined throughout the day driven by the within-hour trends observed at Hudhekede (Figure 2.5d-f, Table A6). Similarly, sub-daily FO declined throughout the study, however, the opposite trend was observed at Farikedede where the proportion of hours per day in which whitetip were identified increased (Figure 2.5a-c, Table A6).

2.4.3 Pelagic thresher *Alopias pelagicus*

Daily pelagic thresher occurrence and relative abundance were higher at Kedevari relative to Hudhekede while hourly occurrence and relative abundance at Kedevari was highest relative to both Farikedede and Hudhekede (Figure 2.7, Table A4, Table A5). Sub-daily and sub-hourly FO was highest at Kedevari and Farikedede compared to Hudhekede (Table A6, Figure 2.5d-f). Additionally, sub-daily FO declined across the study period (Table A6, Figure 2.5a-c). Hourly thresher shark occurrence, as well as relative abundance, was higher between 09:00 and 12:00 during which sub-hourly FO was also highest (Figure 2.7d-f, Fig 2.5, Table A4-A6).

2.4.4 Grey reef shark *Carcharhinus amblyrhynchos*

Grey reef sharks were most commonly observed at Farikede and in higher relative abundances (Figure 2.8). This included hourly and daily occurrence as well as daily relative abundance (Table A4-A5). Sub-daily and sub-hourly FO was also highest at Farikede (Figure 2.5, Table A6). The sub-daily FO increased across the study period and sub-hourly FO peaked between 11:00 and 14:00 (Figure 2.5, Table A6). The hours between 11:00 and 14:00 were also associated with higher grey reef shark relative abundance (Figure 2.8, Table A5).

2.4.5 Tiger shark *Galeocerdo cuvier*

Tiger sharks had higher occurrence and relative abundance at Farikede (Figure 2.9, Table A4, Table A5). Sub-daily and sub-hourly FO differed between the sites with the highest FO observed at Farikede, followed by Kedevvari and Hudhekede (Figure 2.5, Figure 2.9, Table A6). Occurrence, relative abundance, and sub-daily FO declined across days (Figure 2.5, Figure 2.9, Table A4-A6). Furthermore, tiger shark occurrence declined throughout hours of the day at Farikede (Fig 7c). Sub-hourly FO was highest between 09:00 and 12:00, primarily driven by the trend observed at Farikede (Figure 2.5d-f, Table A6).

2.4.6 Silvertip shark *Carcharhinus albimarginatus*

Silvertip sharks were only identified at Farikede. The hourly occurrence of silvertip sharks changed throughout the day with higher occurrences, and sub-hourly FO between the hours 11:00 and 14:00 (Figure 2.10c,d, Figure 2.5f, Table A4, Table A6). Hourly relative abundance changed throughout the day and was highest from 14:00 until evening hours (Figure 2.10d, Table A5). Although we observed an increase in daily occurrence and relative abundance

over the study period, the null was the top model (Table A4, Table A5) likely due to low daily sightings (n = 10 days).

2.5 Discussion

Our study found evidence for species specific influence of site, day and hour on the occurrence, relative abundance, and duration of occupancy on the shark species identified at Fuvahmulah Atoll, Maldives. Overall, 12 species of megafauna were observed, the majority of which were sharks. While an extensive BRUV study conducted on the Great Barrier Reef, a world renowned biodiversity hotspot, identified sharks on 25% of BRUVs, sharks were commonly identified here; present on 95% of the days and 72% of the hours recorded with multiple species identified at each of the sites highlighting the high levels of elasmobranch activity here (Espinoza et al., 2014). Within the top sighted species, both transient apex species (tiger shark and pelagic thresher) and reef-associated mesopredators (whitetip reef shark, grey reef shark, and silvertip shark) were represented. In terms of occurrence (presence-absence), relative abundance (MaxN) and duration of occupancy (sub-daily and sub-hourly FO), site influenced the visitation of all top species except for silvertip sharks which were only detected at Farikede. Our data suggests that Farikede is an ecologically significant site for both reef-associated and transient species while Kedevari is particularly significant for the pelagic thresher.

2.5.1 Site level differences

We found higher occurrences as well as daily relative abundance and duration of occupancy of reef sharks at Farikede. Additionally, the community composition at Farikede was highly associated with the daily occurrence, relative abundance, and duration of occupancy of reef sharks and tiger sharks. This site is likely an ecologically significant area for whitetip reef

sharks, grey reef sharks and silvertips due to the structural complexity that the plateau provides. Areas of greater structural complexity (such as reef slopes) are known to support aggregations of reef-associated species and strong current flow may provide additional benefits (Espinoza et al., 2014, 2015; Lester et al., 2022; Vianna et al., 2013). The steep coral-covered reef provides habitat for benthic-associated species such as the whitetip and the proximity to open ocean currents and upwelling supports primary productivity which provides ample prey opportunities for sharks. It's unsurprising that silvertip sharks were identified only at Farikede. Although the ecology of silvertip sharks is not well known, previous research has suggested the species prefers offshore habitats that are near coral reefs, and additionally show strong associations with specific reef features, such as slopes (Espinoza et al., 2014). Espinoza et al., (2015) revealed that "hotspots" for both silvertips and grey reef sharks are located in areas of stronger current flow. In addition to Farikede, whitetip reef sharks were found at higher occurrences across hours at Hudhekede, where they were also the most frequently observed species. On the Great Barrier Reef, whitetip reef sharks were found in a variety of habitats but were observed in greater numbers on reef slopes (Rizzari et al., 2014). It's likely that the northern and southern ends of the island provide ample benthic complexity while simultaneously providing strong current flow to allow whitetip sharks to rest and ventilate.

For tiger sharks, Farikede also appears to be an ecologically significant site. Occurrence and duration of occupancy of tiger sharks was highest at Farikede compared to other sites across days and hours. While there was no spatial effect of relative abundance across hours (likely a result of rare occurrences of $\text{MaxN} > 1$), daily relative abundance values, were highest at Farikede compared to other sites. This result likely reflected the higher occurrences of tiger sharks at Farikede considering 100% of days recorded a tiger shark presence and therefore

models for daily presence and relative abundance models were separate. Other apex predators have been shown to associate with specific sites at oceanic islands. Hearn et al. (2010) demonstrated that hammerhead sharks favoured the southeastern edge of oceanic islands in the Galapagos and suggested that these sites were likely associated with greater prey availability. Alternatively, the southeastern edges might serve as landmarks for transitions between coastal and epipelagic habitats (Hearn et al., 2010). Tiger sharks, like other pelagic sharks, have demonstrated oscillatory diving behaviour to deeper waters for the suspected purpose of navigation, to increase foraging potential, or increase energy and metabolic efficiency (Andrzejaczek et al., 2020; Campana et al., 2011; Lipscombe et al., 2020). In addition to ample prey opportunities, the sloping nature of the plateau at Farikede may offer convenient transitions to these deeper habitats.

In contrast to reef-associated sharks and tiger sharks, the highest occurrence, relative abundance, and duration of occupancy of pelagic threshers was found at Kedevari compared to the other sites. Additionally, the community composition of Kedevari was highly associated with the sub-daily FO of the pelagic thresher. The effect of site for this species is not surprising considering Kedevari has been identified by the dive community as a pelagic thresher cleaning station (IUCN SSC Shark Specialist Group, 2023). However, there was no significant difference between the daily occurrence and daily relative abundance of pelagic threshers at Kedevari compared to Farikede. These results suggest that, on a broad scale, Farikede is additionally important site for threshers which may be used for foraging, or possibly provide additional cleaning opportunities. Although much more common at Kedevari, local dive centres, as well as images analyzed during this analysis, have identified the interaction of cleaner wrasse with pelagic thresher sharks at Farikede (pers obs).

2.5.2 Seasonal patterns

The relative abundance, and sub-daily FO of whitetip reef sharks and grey reef sharks increased throughout the study. However, the occurrence of whitetip reef sharks and grey reef sharks was not affected by date suggesting that, although presence remains consistent across days, these species spend more time at the sites, and in higher numbers. The observed increases were most prominent at Farikede. Similarly, the sub-daily FO of silvertip sharks increased over days modestly, but not significantly at Farikede, while the occurrence and relative abundance of silvertips here was not affected by date. The patterns of activity of silvertip sharks across days were likely difficult to detect considering this species was only sighted on ten days within the study. Grey reef sharks and whitetip reef sharks show high levels of site fidelity across seasons and years in other isolated regions, and therefore identifying consistent occurrence across days of the study was not surprising (Barnett et al., 2012; Vianna et al., 2013). It's likely that these species are using Fuvahmulah Atoll habitats year-round. However, some evidence indicates that site fidelity is sex biased with females more likely to show strong site fidelity (Heupel & Simpfendorfer, 2014; Vianna et al., 2013).

The increase in relative abundance and sub-daily FO towards the latter portion of the study period demonstrated by reef sharks may be a response to changing biotic or abiotic conditions. August was the final month of data collection and additionally coincided with the peak of the Southwest Monsoon period. The Southwest Monsoon season, known as Hulhangu, occurs from May to October, with March and April identified as transition months (Anderson et al., 2011; Harris et al., 2020; Su et al., 2021). During Hulhangu, the southern equatorial counter current joins with the eastward flowing monsoon current (Benny, 2002). In the Southern regions of the Maldives, downwelling is prevalent along the eastern coastline of the Maldives from June

to July (Su et al., 2021). However, upwelling is initiated in June and reaches its maximum in August or September, during which primary productivity peaks (Schulte et al., 1999; Su et al., 2021). Increased primary production during the Southwest Monsoon season influences the site use of reef manta rays in the Maldives (Harris et al., 2020). Additionally, increased foraging opportunities influence reef shark habitat preference (Heithaus et al., 2002; Rizzari et al., 2014; Sims, Witt, et al., 2006).

Alternatively, the increase in daily relative abundance and sub-daily FO could be a result of altered abiotic factors such as oxygen minimum zones and temperature (Gilly et al., 2013; Vianna et al., 2013). During Hulhangu, and especially in August, when upwelling is maximized, oxygen minimum zones may become increasingly shallow limiting the depth accessed by reef sharks (Gilly et al., 2013). While research has shown that upwelling associated with the southwest monsoon season limits the depth of teleost fish and elasmobranchs (Mcilwain et al., 2011), cameras were placed at Farikedede at roughly 55m depth which is near the maximum depth typically occupied by whitetip reef sharks (Fitzpatrick et al., 2011; Tickler et al., 2017). Grey reef sharks can occupy depths up 60-80m (although deeper dives have been recorded) suggesting that maximum depth could be limited for grey reef sharks during upwelling events that affect oxygen minimum zones (Wetherbee et al., 1997; Vianna et al., 2013). Changes in temperature may additionally impact habitat and depth preferences. While pregnant females may prefer warmer temperatures for reproductive development, cooler waters may be exploited to slow digestion rates (Sims, Wearmouth, et al., 2006; Speed et al., 2012). The increase in daily relative abundance and duration of occupancy of reef-associated species throughout the study likely suggests that the southern end of the island offer optimal habitat during towards the peak of

Hulhangu potentially providing increased feeding opportunities, or optimal conditions for physiological process.

The daily relative abundance, and sub-daily FO of tiger sharks and pelagic threshers declined throughout the study, although declines in pelagic thresher relative abundance were modest and not significant. In addition to daily relative abundance and sub-daily FO, the daily occurrence of tiger sharks also declined. However, we found no effect of date on the occurrence of the pelagic thresher suggesting that the presence of pelagic threshers at Fuvahmulah remains consistent throughout the study period. Ocean currents, water temperature and prey distribution are known drivers of tiger shark movement patterns with complex individual variability in long range migrations (Lipscombe et al., 2020; Werry et al., 2014). As oceanic waters becoming increasingly productive towards the peak of the southwest monsoon season, tiger sharks may be increasingly utilizing offshore areas which may provide alternative areas of high productivity for foraging, or perform long range migrations to and from oceanic islands for pupping or mating (Lea et al., 2018; Werry et al., 2014). Furthermore, the community composition of Fuvahmulah Atoll changed throughout the study period. Although long term studies are needed to tracking visitation patterns across all seasons and throughout multiple years, this indicates that some species may be seasonal visitors to Fuvahmulah Atoll, with a higher level of diversity occurring during monsoon transition months. Multiyear telemetry studies in this area could provide a more detailed understanding of migratory behaviours and additionally identify species that may not have been present during the period of the current study.

Our results suggest that pelagic threshers, however, remain around Fuvahmulah reefs. The observed decline in sub-daily FO suggests a potential behaviour change wherein pelagic threshers may be partaking in less, or shorter, cleaning events with investment in other activities

such as feeding during which pelagic threshers may be utilizing deeper habitats with sightings occurring when pelagic threshers leave the mesopelagic zone to thermoregulate. However, one study tracked the movement patterns of one juvenile male for 15 days and found no evidence of thermoregulatory behaviour (Arostegui et al., 2020). Alternatively, pelagic threshers may be cleaning at other areas of Fuvahmulah, such as on the east side of the island, which was inaccessible for monitoring during this study. Some evidence indicates that males and females may use oceanic and coastal habitats differently (Polo-Silva et al., 2013), therefore, more research should be done to determine potential sex differences in sightings and habitat use of pelagic threshers in Fuvahmulah Atoll.

2.5.3 Diurnal patterns

Reef and apex sharks demonstrated species-specific trends across hours of the day. Hour had no effect on the occurrence of grey reef sharks suggesting grey reef sharks use Fuvahmulah Atoll habitats consistently throughout the day. Grey reef sharks spent higher proportions of time between 11:00 and 14:00, during which higher relative abundances were also found. Silvertip occurrence and sub-hourly FO trailed this peak in grey reef shark activity demonstrated peaks between the hours of 10:00-15:00. Additionally, silvertip relative abundance increased throughout the day. Previous studies have documented the cyclical pattern of daily depth usage of grey reef sharks and silvertip sharks (Barnett et al., 2012; Beauvais et al., 2024; Speed et al., 2011; Vianna et al., 2013). While sharks utilize shallow habitats during dawn and dusk, during the day reef sharks preferentially use deeper waters of around 45m depth adding support to the hypothesis that reef sharks may move into shallow habitats during dawn and dusk for increased foraging opportunities, or to optimize thermal preferences (Beauvais et al., 2024; Speed et al., 2011; Tickler et al., 2023; Vianna et al., 2013). However, since grey reef occurrence remained

consistent across hours our results suggest that the species is present at depth throughout the day but aggregations peak in the afternoon. An aggregation of adult female grey reef sharks in Australia showed a similar pattern wherein peaks in activity were observed at 14:00 and were suspected to have reproductive importance (Speed et al., 2011). Tagging studies in which shark demographics are recorded could lend insight into the potential mechanisms behind aggregations and peaks in sightings. Although grey reef sharks and silvertip sharks displayed similar peaks in activity, whitetip reef sharks demonstrated declines throughout the day in occurrence, relative abundance, and sub-hourly FO. These declines were largely influenced by the activity observed at Hudhekede and may reflect diel movements in shallower or deeper water throughout the day. Alternatively, laboratory studies on whitetip reef sharks indicate that behavioural activity peaks at night, therefore, sightings of this species in the morning hours may be higher if whitetip reef sharks are beginning to diminish activity levels early in the day (Whitney et al., 2007).

Tiger shark occurrence and sub-hourly FO declined throughout the day at Farikede. While the opposite trend was observed at Hudhekede and Kedevari, sightings at these locations were low relative to Farikede. Tiger sharks have demonstrated variable deep diving behaviours wherein individuals make near vertical descents (Vaudo et al., 2014). While recent studies have shown no diel pattern of diving behaviour in tiger sharks, our results indicated that dives, and subsequent returns to shallower water, may be occurring more frequently in the early hours of the day (Hammerschlag et al., 2017; Holmes et al., 2014; Meyer et al., 2009). Other apex predator shark species, such as scalloped hammerheads, as well as reef sharks, have shown distinct diurnal behaviour therefore, monitoring species over 24-hour periods would allow a better resolution of activity patterns and the potential drivers (Speed et al., 2011; Hoffmayer et al., 2013; Ketchum et al., 2014).

Pelagic threshers demonstrated distinct peaks in occurrence, relative abundance and sub-hourly FO at the sites between the hours of 9:00 and 12:00. These trends were observed at Farikede and Kedevari however, the interaction of hour and site was likely not significant due to low sightings at Hudhekede. Limited studies exist on pelagic thresher ecology and movement patterns, however a juvenile pelagic thresher that was satellite tagged in the Red Sea showed distinct diurnal migrations and remained in the mesopelagic zone (200m-300m depth) throughout daylight hours (Arostegui et al., 2020). The patterns of activity in the current study reflect distinct patterns of cleaning station use. To date, one study has examined the cleaning patterns of pelagic threshers at a coastal seamount in the Philippines (Oliver et al. 2013). Our results corroborate Oliver et al. (2013) by identifying more frequent visitations to cleaning stations in the morning hours, followed by a gradual decline in cleaning behaviour throughout the day. Additionally, Oliver et al. (2013) describes pelagic thresher posing behaviour as “circular stance swimming”; a behaviour which is meant to promote cleaner fish inspections. Circular stance swimming was commonly observed in the timelapse footage collected from Kedevari (pers obs). Higher relative abundance coinciding with the peaks in occurrence indicates that multiple thresher sharks are simultaneously using the cleaning station. This suggests that there are peak times wherein cleaning is more beneficial to the species, potential driven by elevated cleaner fish hunger levels which occur in the morning hours (Côté & Molloy, 2003).

2.5.4 Conservation implications

Our results suggest that Farikede is a significant site for the majority of Fuvahmulah’s elasmobranch community, and developing management plans should consider the importance of this site for reef-associated species as well as for migratory species which may depend on the site at various times of the year. Furthermore, resource managers should consider increasing

protective efforts at Kedevari, a site of high ecological importance for the pelagic thresher. Kedevari may be, additionally, a site of global importance considering it is the only identified pelagic thresher cleaning station in the Western Indian Ocean (IUCN SSC Shark Specialist Group, 2023). Future research should aim to conduct long-term monitoring at Fuvahmulah Atoll to identify migratory species that may not be present in this study, but also dependent on Fuvahmulah Atoll reefs.

Our results provide evidence that Fuvahmulah Atoll is a significant habitat for both oceanic and reef-associated elasmobranchs, both of which have experienced recent widespread population declines (Baum et al., 2003; Baum & Myers, 2004; MacNeil et al., 2020b; Pacoureau et al., 2021; Simpfendorfer et al., 2023). Although MPAs, when regulated and enforced, may provide resilience to resident reef shark populations with small home ranges, oceanic or transient populations may be continually exposed to the impacts of fisheries and therefore receive minimal benefits, if any, from MPA designation (Heupel et al., 2014; White et al., 2017; Albano et al., 2021; Simpfendorfer et al., 2023; Goetze et al., 2024). A more detailed understanding of when and how oceanic or migratory species use remote atolls is required to inform MPA design for the protection of key species and important time points (García-Barón et al., 2019; Graham et al., 2016). However, international legislation which regulates fisheries activities will likely be required to protect transient species. Some remote atolls may have experienced an inflated abundance of reef-associated mesopredators due to a loss of transient apex predators (Heupel et al., 2014). Isolated coral reefs, which lack a history of intense exploitation and low human population, may offer refuge for elasmobranch communities which more closely represent historical communities where apex and reef-associated sharks exist together (Barnett et al., 2012; Goetze et al., 2024; Nadon et al., 2012). Recently, Fuvahmulah Atoll was declared an Important

Shark and Ray Area by the IUCN acknowledging the critical importance of the island's reefs for elasmobranch species (IUCN SSC Shark Specialist Group, 2023). This study presents the first detailed findings of the island's elasmobranch community and provides species-specific information that can be used to inform future research directions and management strategies in the area. Since protected populations may help to rebuild populations in decline, offering increased protection and enforcement to the elasmobranch community in Fuvahmulah Atoll may work to increase the global resilience of sharks and rays (Simpfendorfer et al., 2023; Jorgensen et al., 2022).

2.6 Tables and Figures

Table 2.1. Summary of the taxonomy, IUCN Red List status, population trend on the IUCN Red List (Version 2022-2), frequency of occurrence (FO) and relative abundance (MaxN) of the megafauna species observed on remote timelapse cameras.

Species	Common Name	IUCN ^a	Population Trend	FO	MaxN ^b	FO hr ^c	MaxN hr ^c	FO day ^d	MaxN day ^d
<i>Triaenodon obesus</i>	Whitetip reef shark	VU	↓	4.17x10 ⁻³	5	0.44	1.28	0.89	1.89
<i>Alopias pelagicus</i>	Pelagic thresher shark	EN	↓	1.68x10 ⁻²	3	0.41	1.27	0.83	1.67
<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	EN	↓	7.66x10 ⁻³	21	0.32	2.38	0.78	3.98
<i>Galeocerdo cuvier</i>	Tiger shark	NT	↓	8.98x10 ⁻⁴	2	0.17	1.01	0.67	1.02
<i>Carcharhinus albimarginatus</i>	Silvertip shark	VU	↓	9.39x10 ⁻⁴	6	0.050	1.85	0.16	2.40
<i>Sphyrna lewini</i>	Scalloped hammerhead	CR	↓	1.83x10 ⁻⁴	7	0.042	1.27	0.32	1.40
<i>Mobula birostris</i>	Oceanic manta ray	EN	↓	1.50x10 ⁻⁴	2	0.023	1.06	0.19	1.08
<i>Eretmochelys imbricata</i>	Hawksbill sea turtle	CR	↓	2.46x10 ⁻⁴	1	0.019	1.00	0.16	1.00
<i>Aetobatus ocellatus</i>	Spotted eagle ray	VU	↓	2.09x10 ⁻⁴	4	0.013	2.10	0.079	2.20
<i>Rhincodon typus</i>	Whale shark	EN	↓	3.31x10 ⁻⁵	1	0.0054	1.00	0.063	1.00
<i>Torpedo sinuspersici</i>	Variable torpedo ray	DD	?	1.23x10 ⁻⁵	1	0.0027	1.00	0.032	1.00
<i>Pastinachus sephen</i>	Cowtail stingray	NT	↓	3.68x10 ⁻⁶	1	0.0013	1.00	0.016	1.00

^aAbbreviations; LC, Least Concern; NT, near threatened; VU, vulnerable; EN, endangered; DD, data deficient; FO, frequency of occurrence (i.e proportion of images observed on)

^bMaxN, maximum number of individuals observed per species across images collected.

^cFrequency of occurrence measured by the proportion of hours species were observed on out of total recorded hours; MaxN averaged across hours where species occurred

^dFrequency of occurrence measured by the proportion of days species were observed on compared to total day recorded; MaxN averaged across days where species occurred

Table 2.2. Results of permutational multivariate analysis of variance (PERMANOVA) tests examining the effects of site and study period category on megafauna community composition. Sub-daily FO is measured by the proportion of one-hour intervals in a day that species were sighted on each day at the sites. Note that F values reflect the pseudo F statistic.

	Site	Date Category (early-mid-late)
Occurrence and relative abundance	F = 15.28 R ² = 0.28 <i>p</i> = 0.001	F = 4.67 R ² = 0.07 <i>p</i> = 0.001
Sub-daily FO	F = 28.06 R ² = 0.31 <i>p</i> = 0.001	F = 10.35 R ² = 0.083 <i>p</i> = 0.001

Table 2.3. Results of permutation test for homogeneity of multivariate dispersions of megafauna community composition within site and study period category. Dispersion is measured from the centroid. Sub-daily FO is measured by the proportion of one-hour intervals that species were sighted on each day at the sites.

	Site	Date Category (early-mid-late)
Occurrence and relative abundance	F = 1.90 <i>p</i> = 0.154	F = 4.15 <i>p</i> = 0.017
Sub-daily FO	F = 34.52 <i>p</i> = 0.001	F = 3.15 <i>p</i> = 0.059

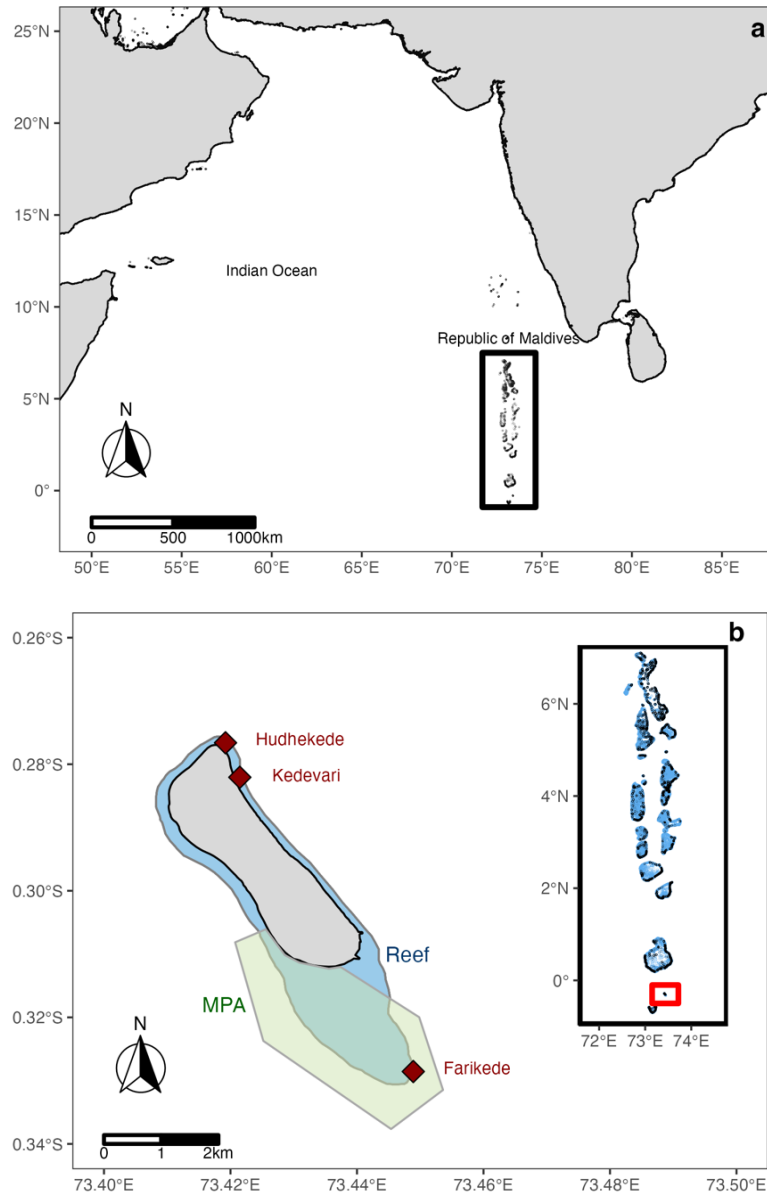


Figure 2.1. Map of Fuvahmulah Atoll (a) showing the loaction of camera deployment sites and position relative to designated marine protected area. The position of Fuvahmulah Atoll (red box) relative to the Republic of Maldives is shown (a) as well as the location of the Maldives within the western Indian Ocean (b).

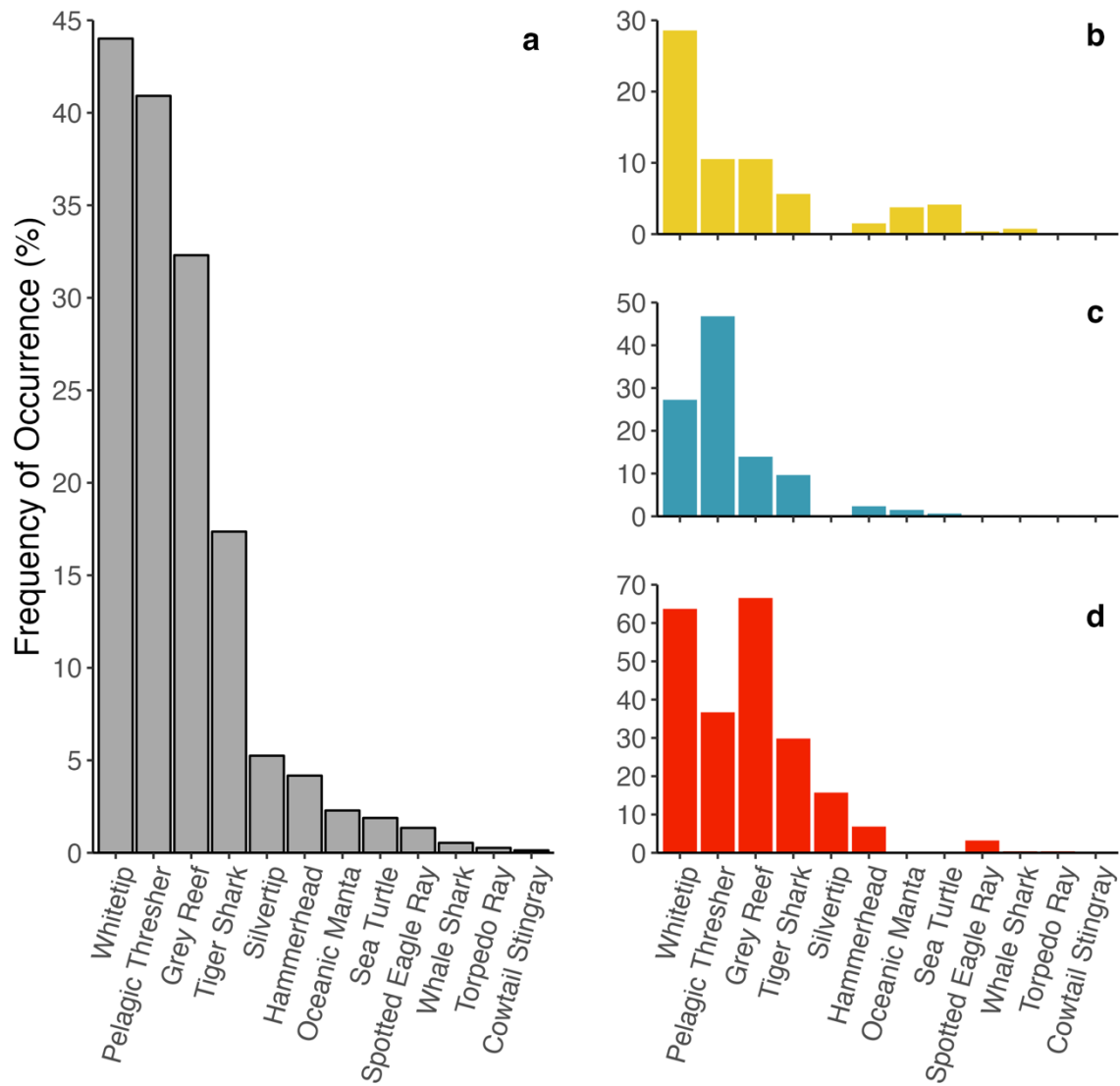


Figure 2.2. Frequency of occurrence measured by the proportion of hours that species were observed on (presence-absence) out of the total number of hours recorded overall (a) and at Hudhekede (b), Kedevari (c), and Farikedede (d). All values represent a percentage. Note the different y axis values.

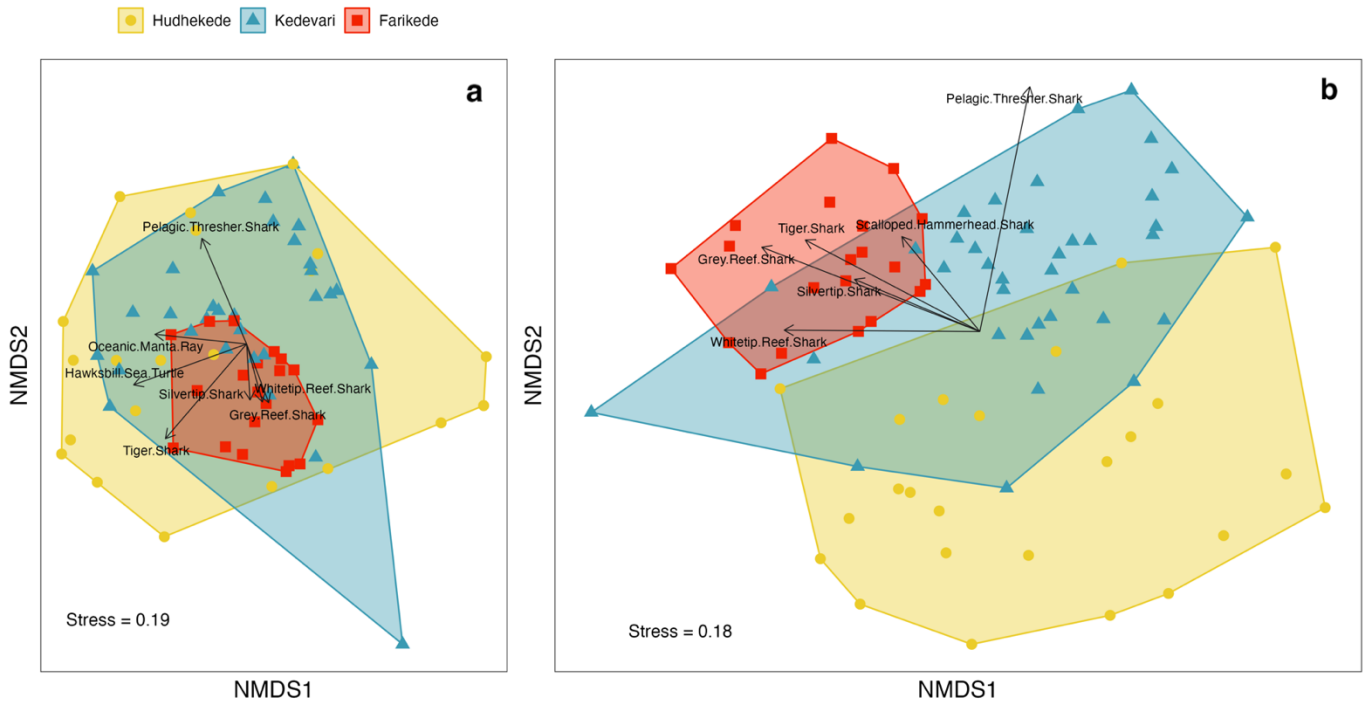


Figure 2.3. NMDS of megafauna community composition of surveyed sites (Hudhekede, Kedevari and Farikede) on Fuvahmulah Atoll, Maldives, according to (a) species' daily occurrence and relative abundance, and (b) sub-daily frequency of occurrence. Each point represents one day of recorded observations at the sites where at least one species was present ($n = 81$). Species displayed represent statistically significant species scores ($p < 0.05$).

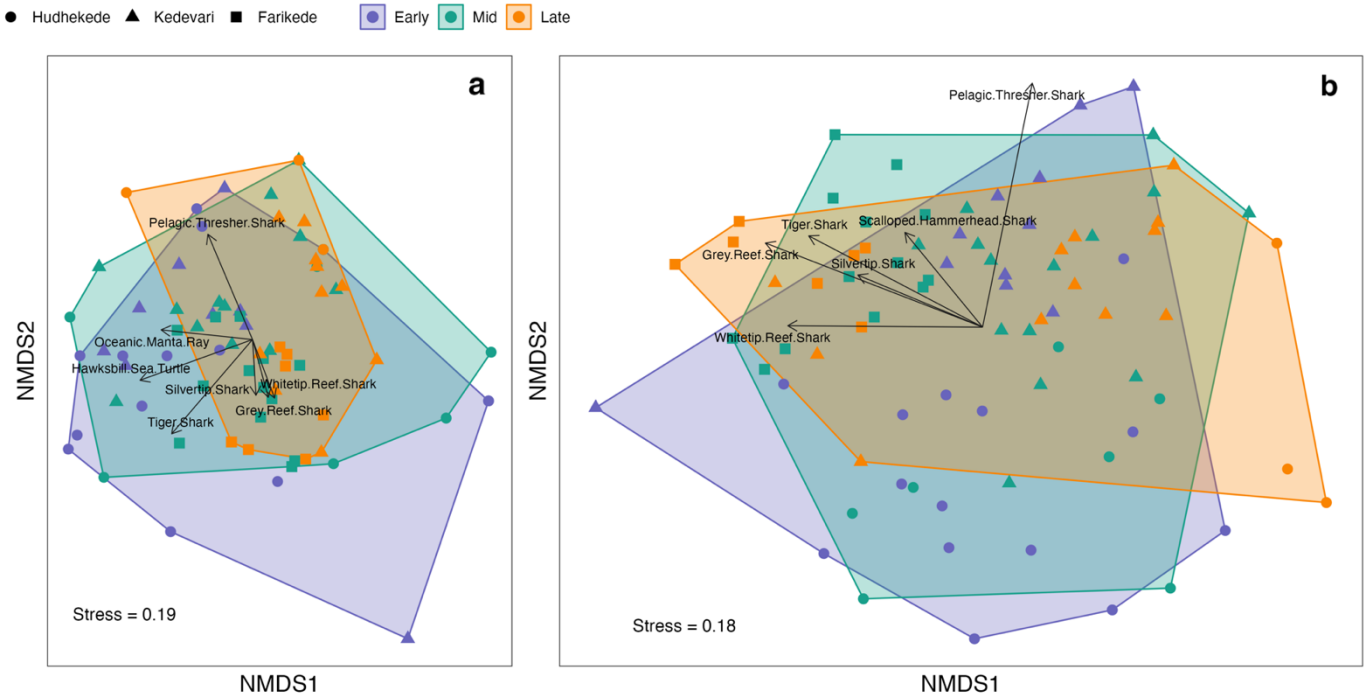


Figure 2.4. NMDS of megafauna community composition of early (March-April), mid (May-June) and late (July-August) date categories on Fuvahmulah Atoll, Maldives according to (a) species' daily occurrence and relative abundance and (b) sub-daily frequency of occurrence. Each point represents one day of recorded observations at the sites where at least one species was present ($n = 81$). Species displayed represent statistically significant species scores ($p < 0.05$).

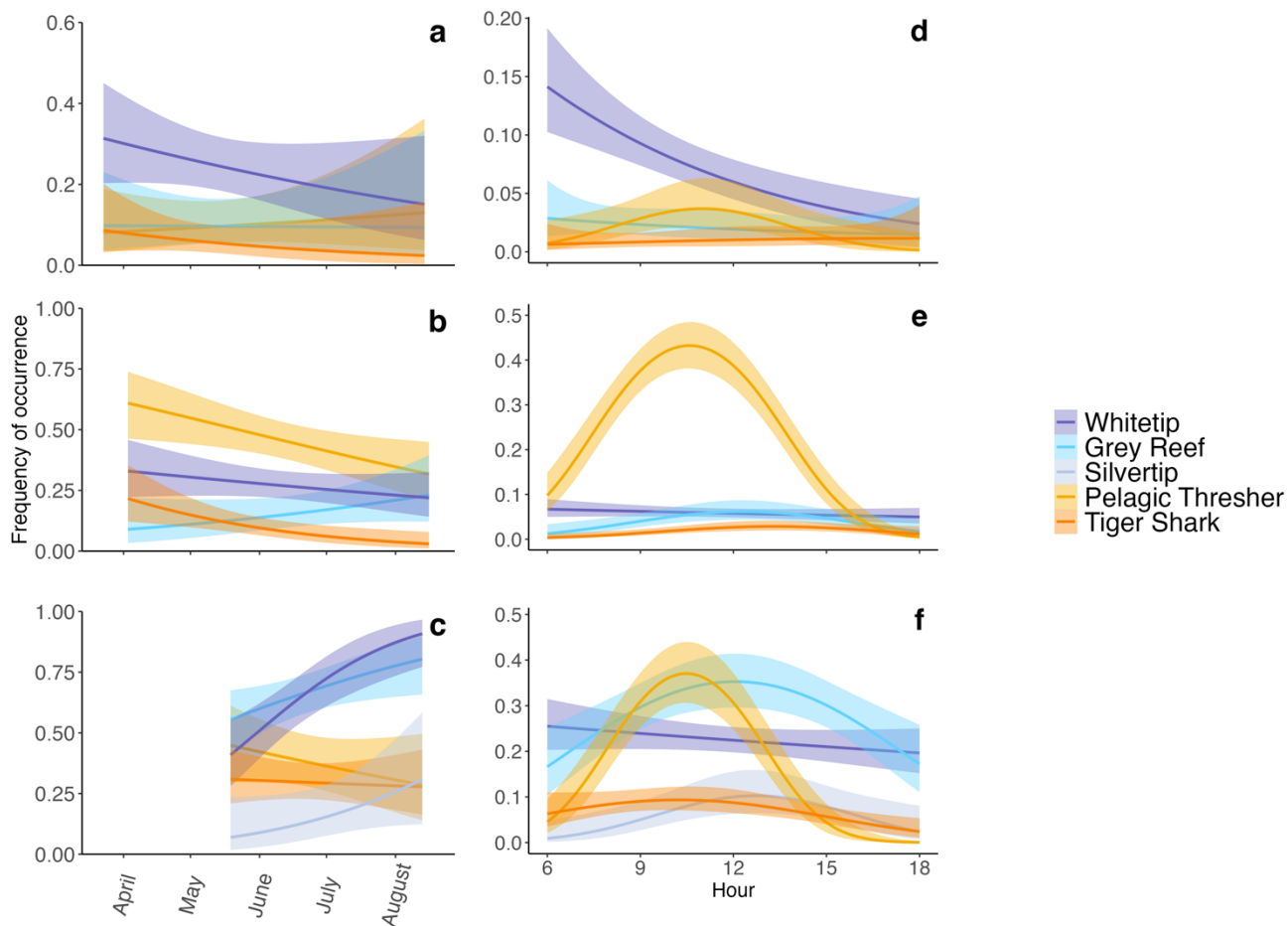


Figure 2.5. Linear regression of sub-daily (a,b,c) and sub-hourly (d,e,f) frequency of occurrence at Huhekede (a,d), Kedevari (b,e) and Farikedede (c,f). Shaded areas represent the 95% confidence interval. Reef sharks (whitetip, grey reef and silvertip) are shown in cool colours while transient species (pelagic threshers and tiger sharks) are shown in warm colours. Sub-daily frequency of occurrence is measured by the proportion of hours within each day in which species were observed (a-c). Sub-hourly frequency of occurrence is measured by the proportion of 10min intervals within each hour (d-f) in which species were observed on. Patterns of the five most frequently sighted species are shown. Daily records at Farikedede (c) did not occur until mid-May due to limited site access.

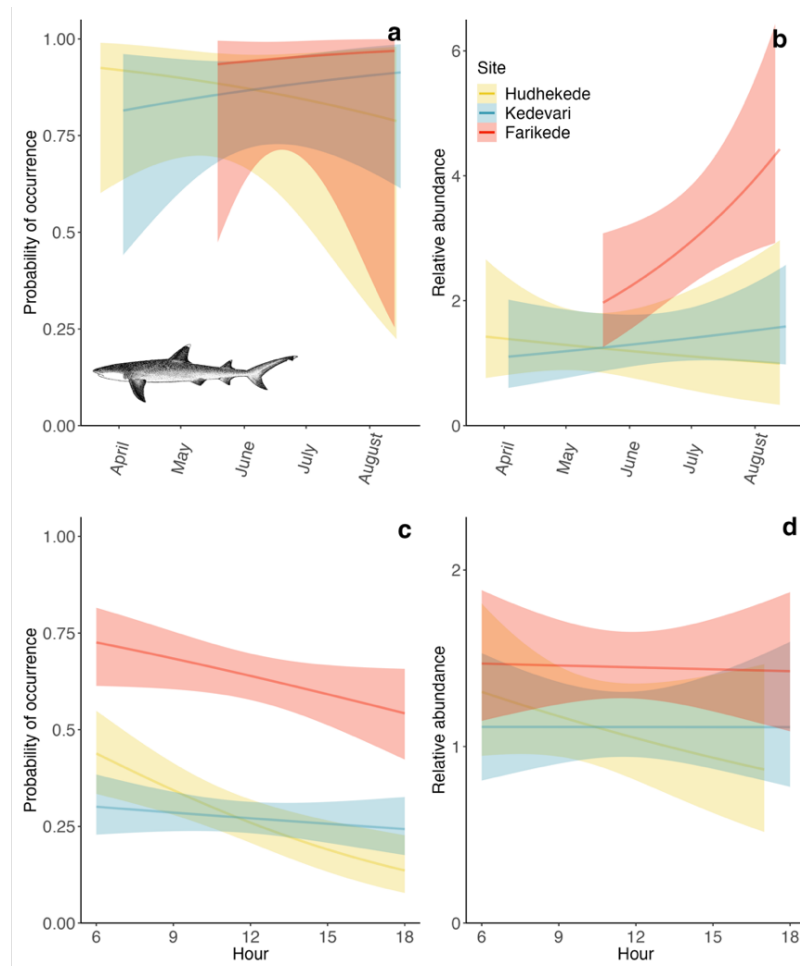


Figure 2.6. The probability of occurrence (presence-absence) and predicted relative abundance (MaxN) of whitetip reef sharks (*Triaenodon obesus*) across days (a,b) and across hours (c,d) at Hudhekede, Kedevari, and Farikede. Lines represent linear regressions and shaded areas represent 95% confidence intervals. Daily records at Farikede (a,b) did not occur until mid-May due to limited sight access.

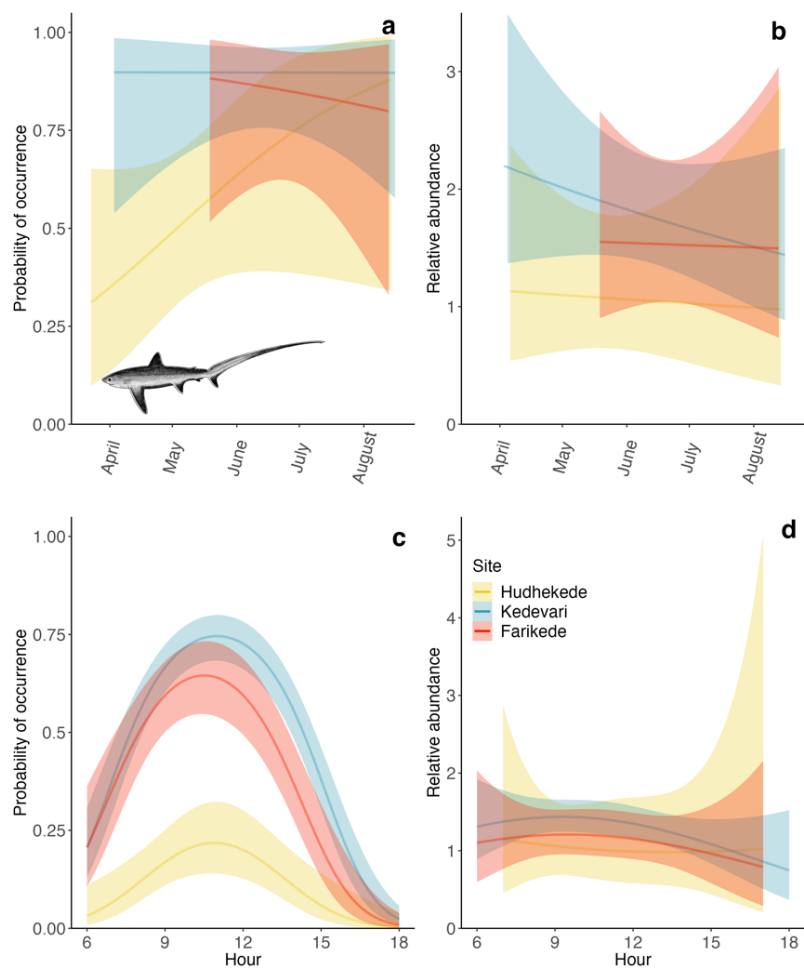


Figure 2.7. The probability of occurrence (presence-absence) and predicted relative abundance (MaxN) of pelagic threshers (*Alopias pelagicus*) across days (a,b) and across hours (c,d) at Hudhekede, Kedevari, and Farikede. Lines represent linear regressions and shaded areas represent 95% confidence intervals. Daily records at Farikede (a,b) did not occur until mid-May due to limited sight access.

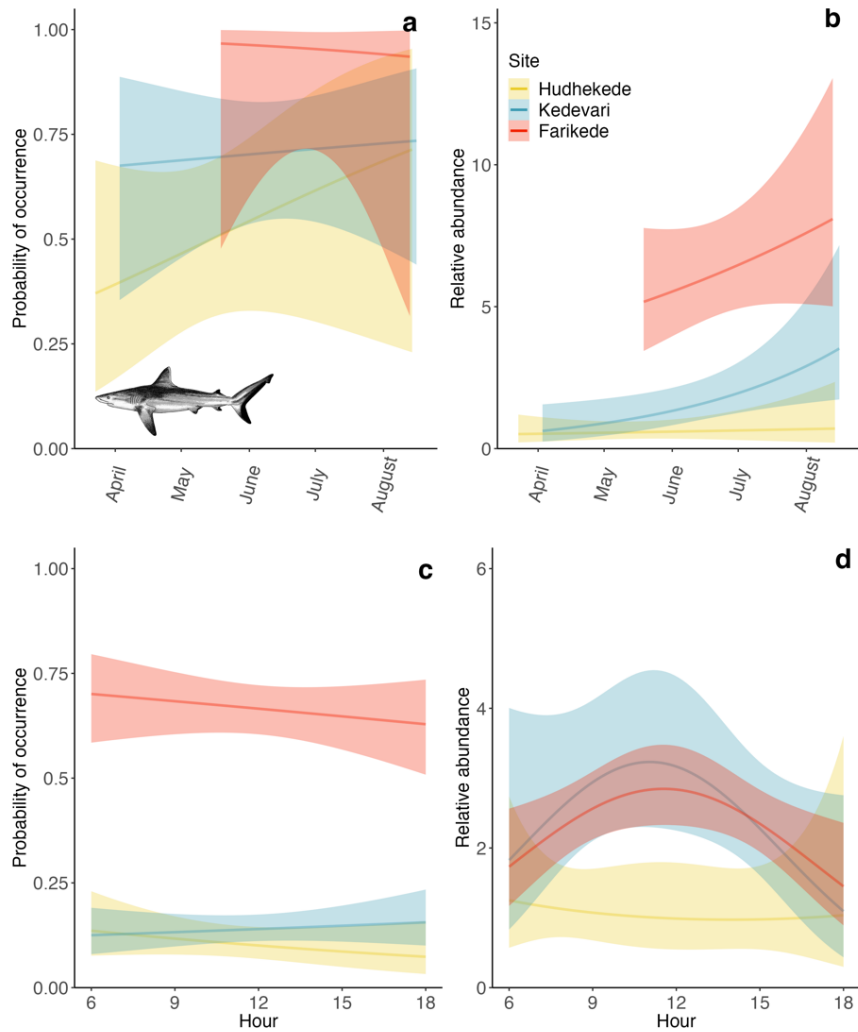


Figure 2.8. The probability of occurrence (presence-absence) and predicted relative abundance (MaxN) of grey reef sharks (*Carcharhinus amblyrhynchos*) across days (a,b) and across hours (c,d) at Hudhekedde, Kedevari, and Farikede. Lines represent linear regressions and shaded areas represent 95% confidence intervals. Daily records at Farikede (a,b) did not occur until mid-May due to limited sight access.

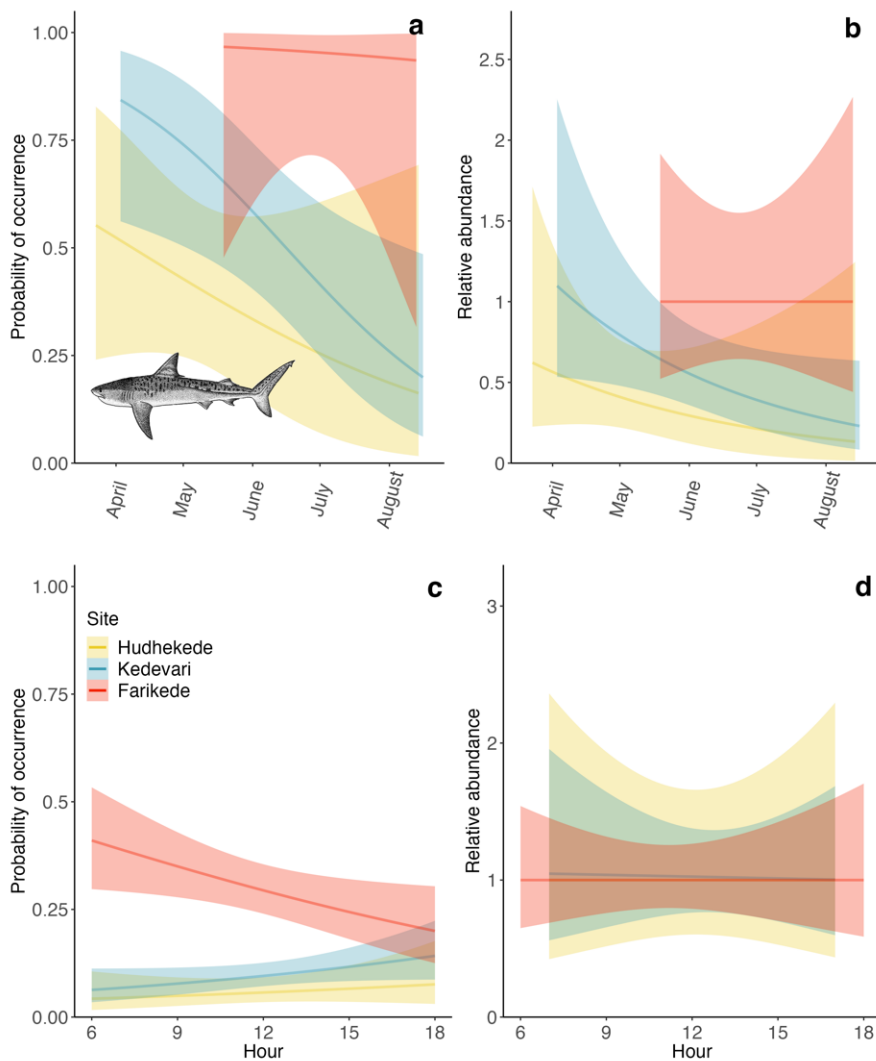


Figure 2.9. The probability of occurrence (presence-absence) and predicted relative abundance (MaxN) of tiger sharks (*Galeocerdo cuvier*) across days (a,b) and across hours of the day (c,d) at Hudhekede, Kedevari and Farikede. Lines represent linear regressions and shaded areas represent 95% confidence intervals. Daily records at Farikede (a, b) did not occur until mid-May due to limited site access.

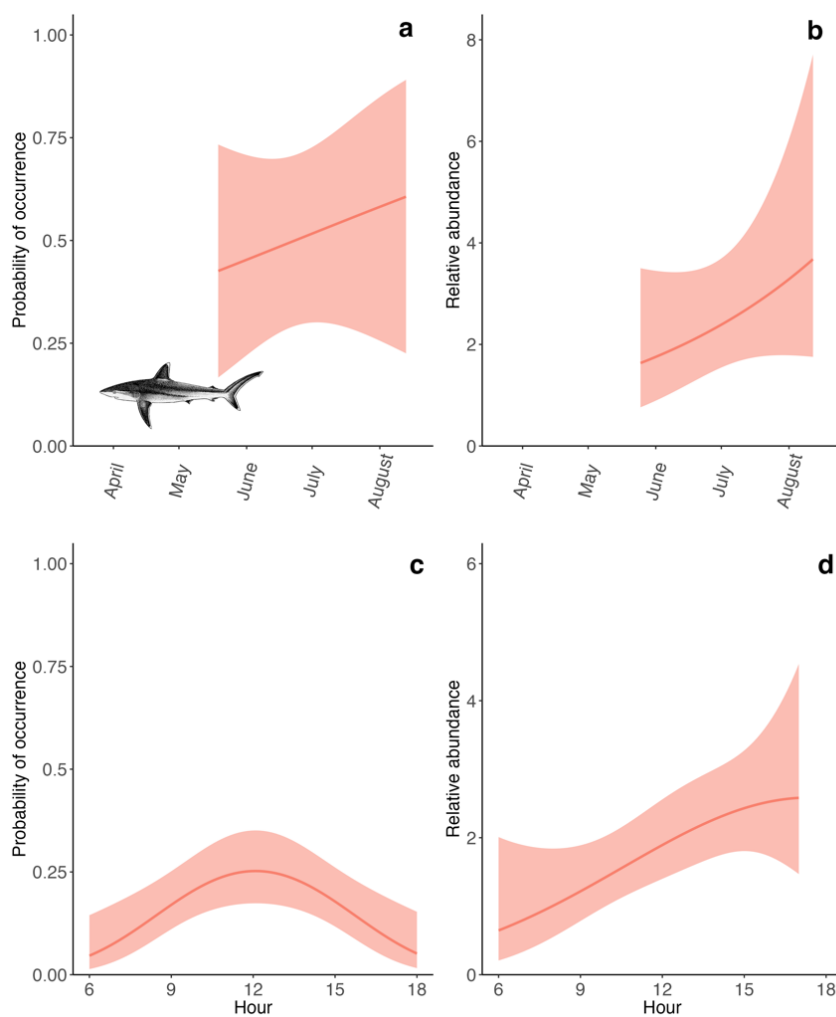


Figure 2.10. The probability of occurrence (presence-absence) and predicted relative abundance (MaxN) of silvertip sharks (*Carcharhinus albimarginatus*) across days (a,b) and hours (c,d) at Farikede. Silvertip sharks were only identified at Farikede. Lines represent linear regressions and shaded areas represent 95% confidence intervals. Daily records at Farikede (a, b) did not occur until mid-May due to limited site access.

Chapter 3 - The potential contribution of tourism to a newly designated UNESCO Biosphere Reserve in the Maldives

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3.1 Abstract

Tourism is increasingly used to finance conservation and accounts for a significant portion of economic growth in many island nations, including the Republic of Maldives. Abundant and diverse marine life is a critical component of the Maldives' tourism, with snorkelling and diving identified as the most popular tourist activities. Strategic management plans are being developed throughout the Maldives to safeguard marine ecosystems while supporting economic growth. However, it is unclear if dive tourists are willing to contribute financially to help conserve the biodiversity upon which their tourism depends. Known as 'the Galápagos of the Maldives,' Fuvahmulah Atoll, a recently designated UNESCO Biosphere Reserve, has recently experienced a rise in dive tourism due to improved accessibility to and awareness of its abundant and diverse shark and ray megafauna. Here, we sought to inform policy design by examining tourists' willingness to pay for increased conservation action on the atoll. Working collaboratively with a local tourist operator, we conducted a stated preference survey to assess tourists' environmental attitudes, willingness to pay for an entrance fee to Fuvahmulah, and preferences for conservation measures proposed by the community. Virtually all (97%) tourists were supportive of paying a one-time "Reserve" entrance fee. On average, tourists were willing to pay US\$58 per person. Tourists preferentially supported waste management and marine protected area management over community education and marine research facilities. Encounters with tiger sharks or pelagic threshers on Fuvahmulah Atoll reef positively impacted the amount tourists were willing to pay. As committed members of the dive community, visitors to Fuvahmulah Atoll highly value marine conservation, and their financial support creates unique opportunities to safeguard biodiversity and ensure the sustainability of the nation's largest industry.

3.2 Introduction

Nature-based tourism, defined as travel motivated by experiences in nature, has been increasing globally and is considered one of the fastest-growing sectors of the tourism industry (Goodwin, 1996; Balmford et al., 2009, 2015). By diversifying the livelihoods of communities living close to protected areas, tourism offers alternative sources of income. Tourism has created a socioeconomic shift in many regions from dependence on extractive industries such as fishing (Diedrich, 2007). Furthermore, the contribution of nature-based tourism to economic growth has motivated nations to protect species at risk of extinction and their habitats (Van Oosterzee, 2000; Hall, 2010). However, tourism does not intrinsically benefit conservation and, in some cases, has also been linked to negative consequences for ecosystems and wildlife (Brandt & Buckley, 2018; Stronza et al., 2019).

Although there is potential for increased conservation achievement through tourism, negative human impacts persist when local communities or sectors fail to receive benefits or when management plans fail to protect sensitive species and ecosystems. For example, while overfishing is the primary threat to shark and ray populations, in the case of shark and ray tourism in Indonesia, economic benefits have not reached fishers, and thus, shark and ray populations continue to be exploited (Mustika et al., 2020). Butler (1980) originally described how tourism may operate to the detriment of the environment. Indeed, the negative impacts of unregulated tourism on ecosystems and wildlife have been well documented (Trave et al., 2017). On coral reefs, scuba diver behaviour can cause direct damage to corals due to physical contact, increased coral disease susceptibility, and increased sedimentation, leading to localized bleaching and tissue loss (Cerutti-Pereyra et al., 2022; Hawkins & Roberts, 1992; Krieger & Chadwick, 2013; Lamb et al., 2014). Ecosystems have also experienced degradation through the

development and pollution associated with tourism. In addition to habitat loss or degradation, tourism can impact wildlife by causing stress and altering wildlife behaviour. Tourist behaviour interrupts manta ray foraging and has been associated with increased behavioural stress responses in green sea turtles, as well as increased parasite loads and compromised immune systems in stingrays (Tapper, 2006; Semeniuk et al., 2009; Griffin et al., 2017; Murray et al., 2020). Without effective management, the very resources that attracted tourism in the beginning may be degraded or destroyed, leading to a collapse of the tourism industry.

As a method of increasing the sustainability of tourism to natural areas and ensuring tourism generates conservation benefits, protected areas may impose entrance fees to visitors, which directly fund practices that improve conservation outcomes (Depondt & Green, 2006; Terk & Knowlton, 2010; Brown et al., 2023). The contribution of visitor fees to marine protected areas (MPAs) is especially important, considering funds for long-term monitoring and enforcement are limited yet critical for MPA success (Peters & Hawkins, 2009; Bohorquez et al., 2019; Brown et al., 2023). Snorkelers and divers are MPA users who typically place a high value on the state of marine life and, therefore, represent an opportunity to financially support the protection and conservation of marine ecosystems and wildlife (Peters & Hawkins, 2009; Grafeld et al., 2016). This may be especially true for experienced divers, who may be more aware of the increasing anthropogenic impacts on marine ecosystems (Luo & Deng, 2008; Nisbet et al., 2009; Malpica-Cruz et al., 2017).

The amount that tourism could potentially contribute to MPAs is often not fully realized (Depondt & Green, 2006; Peters & Hawkins, 2009). A comparative study investigating tourists' willingness to pay entrance fees at MPAs on a global scale found that the average willingness to pay is consistently higher than current charges if any charges are implemented at all (Peters &

Hawkins, 2009). This suggests that tourists place a high value on the management of marine ecosystems and are indeed willing to contribute to create a more sustainable tourism industry.

Tourism is the main economic driver in the Republic of Maldives (Maldives Ministry of Tourism, 2023), and the health of the natural environment plays a central role in maintaining the country's tourism industry. Snorkelling and diving are rated the most popular activities among tourists visiting the island nation, and the economic benefit derived from tourism has historically depended on tourist satisfaction with the marine environment (Ali & Sinan, 2014; Ministry of Tourism, 2022). In the 1990s, shark fishing noticeably depleted shark populations, which resulted in significant losses to the dive tourism industry (Ali & Sinan, 2014). In response to the decline in tourism, the Government of the Maldives declared the country a shark sanctuary, offering legal protection to sharks and rays from fisheries exploitation in 2010 and 2014, respectively (Government of the Maldives President's Office, 2010; EPA, 2014; Ali & Sinan, 2014; Ward-Paige, 2017). The income generated in the Maldives from diving has increased substantially in recent years, with shark and ray diving collectively contributing US\$29.8 million per year in direct revenue (Anderson et al., 2011b; Cisneros-Montemayor et al., 2013; O'Malley et al., 2013; Zimmerhackel et al., 2019).

Fuvahmulah Atoll is a remote, single-island atoll in the southern Maldives nicknamed "Shark Island" for its diverse and abundant shark and ray megafauna. Dive tourism has increased rapidly in this location due to improved access to this region and awareness of the elasmobranch visitation. In recognition of the significant biodiversity in terrestrial and marine ecosystems, Fuvahmulah Atoll was declared a UNESCO Biosphere Reserve in 2020 (UNESCO, 2020). However, management plans for the Biosphere Reserve and the MPA within it are still being developed. While there is a recognized need for long-term funding strategies which support

conservation on the island, considerable uncertainties remain about the potential impact of tourist fees on the tourism industry.

In July 2023, Fuvahmulah City Council announced the implementation of a tourist fee for dive tourism activities. The fee structure aimed to implement charges to both international and resident divers. Regulations stated that those operating from international vessels would be charged US\$200 per guest for a 15-day period. Safari vessels and diving schools from outside of Fuvahmulah but within the Maldives and operators within Fuvahmulah would be charged US\$55 and US\$40 per person, respectively, for the same duration. The regulations stated that guests who are citizens of the Maldives and work permit holders would be charged less. Significant resistance from the dive community of Fuvahmulah occurred following the announcement of the fee implementation. News articles reported that community members voiced concerns about the sustainability of the tourism industry with the specified regulations in place and the lack of community consultation in designing the management plan (“Fuvahmulah Mayor Faces Calls to Resign over New Diving Fee,” 2023; Mizyal, 2023; Mohamed, 2023). In August of 2023, the fee implementation was postponed by Fuvahmulah City Council, highlighting the need for more informed policy design and community involvement.

Here, we aim to quantify how much tourists to Fuvahmulah Atoll would be willing to contribute to park entry fees. Additionally, we investigate the factors that impact the willingness to pay, explicitly focusing on tourist preferences and interests in marine conservation and dive tourism activities. Specifically, we ask: 1) are tourists willing to pay to increase conservation measures in Fuvahmulah Atoll? If so, at what value? 2) Do tourists preferentially support some conservation initiatives over others? 3) What factors affect the amount that tourists are willing to contribute? We predict that dive tourists to Fuvahmulah Atoll would be willing to contribute to

conservation in the form of entrance fees and that more experienced divers, as well as those who hold stronger pro-environmental attitudes would be willing to contribute higher fees. By comprehensively understanding visitor demographics and interests, we contribute critical knowledge to developing management plans for protected areas and, more generally, the Fuvahmulah Atoll UNESCO Biosphere Reserve.

3.3 Methods

3.3.1 Study site

The Republic of Maldives has 26 atolls and extends 870km, spanning the equator (Figure 3.1; Stevens & Froman 2018). Fuvahmulah Atoll is one of the most southern atolls, located 494km south of Malé, the capital of the Maldives. Access to Fuvahmulah Atoll was historically difficult before opening a domestic airport in 2011, before which tourist visitation was uncommon (Araujo et al., 2024). The first dive centre opened in 2013; however, eleven dive centres are in operation today, reflecting the increasing recognition of the financial benefits of tourism on the island.

Fuvahmulah divers encounter resident reef shark species and seasonal visitation of transient species including scalloped hammerheads (*Sphyrna lewini*) and oceanic manta rays (*Mobula birostris*). In addition, dive centres advertise frequent encounters with tiger sharks (*Galeocerdo cuvier*) and pelagic threshers (*Alopias pelagicus*). Pelagic threshers frequent cleaning stations on the island's reef which represent the only identified cleaning stations for this species in the Western Indian Ocean (IUCN SSC Shark Specialist Group, 2023).

Multiple protected areas exist on Fuvahmulah Atoll which intend to offer protection from human activities to select sites. In total, there are four protected areas within the Biosphere

Reserve. Three protected were designated in 2012 and include two wetland and mangrove ecosystems (Bandaara Kilhi and Dhandimagu Kilhi) as well as the highly dynamic sand spit (Thundi Area) on the northeast corner (MCCEE, 2024). More recently, an MPA encompassing 6km of the southern reef was designated for which management plans are in development (Figure 3.1; MCCEE, 2024). Management plans for the Biosphere Reserve as well as the protected areas within it aim to safeguard the island's biodiversity and socioeconomic importance.

3.3.2 Survey overview

To better understand tourists' perceptions and attitudes toward marine conservation in Fuvahmulah Atoll, a contingent valuation survey was designed and implemented for international and national island visitors. Contingent valuation is a stated preference method which uses questionnaires to assess the willingness to pay for a change in an environmental good (Arrow et al., 1993; Johnston et al., 2017). Scenarios are constructed to offer alternatives to the status quo. Well-designed and carefully tested questionnaires are expected to reveal respondent's true willingness to pay for a given change (Johnston et al., 2017). Using the contingent valuation method (CVM), we asked if visitors would support the implementation of a one-time "Reserve" entrance fee to Fuvahmulah Atoll and assessed visitors' willingness to pay for initiatives which support marine conservation on the island.

3.3.3 Survey design

The survey design followed the recommendations of Arrow et al. (1993) where possible. Within a single online questionnaire, respondents were provided with a short introduction, including a description of incentives and the privacy policy. This introduction highlighted that

the survey was anonymous, and any information provided for the incentive draw would not be linked with survey responses. The incentives, donated by the Manta Trust, included entries into a draw for either a 1-year Cyclone membership or a Manta Ray Adoption Package. The survey began by asking respondents to identify if they were a Maldivian national visitor, an international visitor, or a resident of Fuvahmulah to filter out any potential participation by the local community. If a local resident was selected, respondents were guided to a thank you message before the survey automatically exited.

Next, knowledge and perceptions of important marine life at Fuvahmulah Atoll, as well as previous interactions with sharks and rays, were assessed through a set of four warm-up questions. This portion of the survey aimed to orient the respondents to the topics covered within the survey, encouraging reflection on current understanding and assessing if perceptions, knowledge, and previous interactions impact stated willingness to pay values (Johnston et al., 2017). Respondents were then guided to either a video or PDF file (determined by a preliminary question asking if limited bandwidth may be an issue) which explained the UNESCO Biosphere designation of Fuvahmulah Atoll and the need for long-term funding strategies to finance marine conservation initiatives on the island. Proposed marine conservation initiatives were presented and explained identically in the video and PDF. Initiatives included community education, waste management, protected areas management, and a marine research and education centre. These initiatives were included based upon consultations prior to survey development with groups from and working within the community, including Fuvahmulah City Council, Pelagic Divers Fuvahmulah, Maldives Manta Conservation Programme, Fuvahmulah Nature Park and Fuvahmulah Surf Association. The current need for these initiatives was clearly outlined,

presenting a baseline or status quo scenario, a critical requirement in stated preference questionnaires (Johnston et al., 2017).

If limited bandwidth was selected before the video, respondents were guided to the PDF alternative, and an internal timer ensured respondents were adequately engaged with the survey material. If respondents were not on limited bandwidth, an additional check occurred after the video played to confirm that respondents could see and hear the video. Respondents were redirected to the timed PDF script if any visual or audio issues were indicated. After explaining each initiative, respondents were told that their responses would be shared with policymakers:

While the following questions seem hypothetical, please remember that your answers will be considered by Fuvahmulah City Council and will impact policy design.

The amount you state may be accepted as the charge for visiting this area in the future.

This statement aimed to strengthen incentive compatibility by demonstrating that the answers can be translated into enforced payments (Cummings et al., 1997). The statement was followed by the willingness to pay question, which included a range slider for respondents to indicate a value from US\$0 to US\$200:

Considering your income and current expenses, slide the bar to indicate how much (USD) you would be willing to pay as a Fuvahmulah Atoll entry fee if those funds were to be divided among the projects outlined in the video?

*This fee would be a **one-off** charge collected by your guest house **once for your trip** rather than a daily fee or a fee per dive.*

All monetary questions included a link to a currency exchange resource (<https://www.xe.com/currencyconverter/>). Respondents were then asked to rate their certainty of their answer on a four-point scale. Respondents who selected a positive value for payment were

asked additional questions to gather information about tourist perceptions of responsibility, price sensitivity, and preferences for the fee distribution across the proposed initiatives. To determine protest bids, those who indicated a zero willingness to pay were asked their reason for doing so. Valid-zero responses included any of the following answers: (i) I feel I cannot afford to pay more to contribute to these conservation initiatives; (ii) I'm not interested in contributing to these conservation initiatives. Alternatively, protest-zeros included responses: (i) I don't believe the money gained by fees will be spent reasonably on conservation initiatives; (ii) I feel the money for these initiatives should come from other places and not from tourists; (iii) I can't decide without more time or information; (iv) I didn't understand the question. Respondents could also select *Other (please specify)* to input an answer that accurately reflects their position, which would be categorized as a valid or protest-zero answer during analysis. This approach maximizes the validity of valuation studies by minimizing potential biases presented in stated preference frameworks (Bishop & Boyle, 2017; Ison et al., 2021).

The next part of the survey investigated the interests, attitudes, and demographics to build visitor profiles and identify covariates that could explain changes to the observed willingness to pay. A trap question, which can be used to assess the attentiveness of respondents, was included at the beginning of this section to ensure that all questions were being carefully read (Oppenheimer et al., 2009).

To ensure all questions are being carefully read, please select manta ray from the list below; (i) whaleshark (ii) mola mola (iii) manta ray (iv) devil ray (v) hammerhead shark.

Any respondents who failed to select the *manta ray* were excluded from the data analysis. The primary reason for an individual's visit to the island was investigated. If respondents identified dive tourism-related activities (such as snorkelling, freediving or scuba-diving),

follow-up questions identified their skill level, commitment to the activity and if they have previously visited Fuvahmulah Atoll for that purpose. We asked if dive tourism visitors had an excursion type preference (reef dives or blue water dives) and if a particular marine organism motivated their trip to Fuvahmulah Atoll. Respondents who were motivated by encounters with marine organisms ranked their top three choices for encounter preference based on species known to occur in this region of the Maldives. We also asked respondents which organisms they had encountered in the area to gauge their potential satisfaction level during their visit. Demographic questions included gender, age, annual income, and education. Finally, environmental attitudes and values were explored by asking about respondents' charitable donation history and using the New Ecological Paradigm scale.

The New Ecological Paradigm scale (NEP) is a standardized set of questions which assess an individual's environmental attitude, and it's commonly incorporated in studies aiming to understand the intrinsic value of environmental goods and services (Dunlap et al., 2000; Dunlap & Van Liere, 1978; Taye et al., 2018). Items of the NEP scale describe worldviews toward humanity's relationship with the natural environment. Respondents were asked to indicate their level of agreement and disagreement with 15 items (Dunlap et al., 2000). Answers were then summed together to categorize each respondent as having a (i) strong dominant social paradigm, (ii) moderate dominant social paradigm, (iii) ambiguous worldview, (iv) moderate ecological worldview, and (v) strong ecological worldview. The complete survey, including the NEP scale questions, is included in **Appendix B**.

The final page of the survey thanked participants and reviewed the details of the available incentives. Participants were reminded that all survey responses are anonymous and that personal details provided for the incentive draw would not be linked to survey responses at any point. A

link to the privacy policy was included followed by a text box where participants could opt to enter their name and email for the incentive draw. Finally, an open text feedback box concluded the survey where participants were given the opportunity to voluntarily share any additional feedback or comments. These comments were reviewed during data analysis to identify any common trends in values or concerns, and identify potential issues with survey completion or interpretation.

The research team designed and pretested the survey on two separate occasions within the University of Victoria between November and December 2022. Pretesting utilized the feedback of 11 people and ensured readability and understanding of scenarios and payment vehicle while minimizing respondent fatigue (Champ et al., 2003). As a result of the pretesting, minor wording changes were made to increase clarity and readability. The final online survey was built by Omnisys and UK marketing consultant, Deep Blue Thinking, and further tested with a group of five people in December 2022. The survey was launched in January 2023, and responses were closely monitored to ensure proper functioning. The first surveys were presented to tourists in Fuvahmulah Atoll by staff of the Manta Trust, who were briefed on project aims and survey distribution and were able to assist respondents with navigating the online platform when required. With a higher rate than expected of incomplete surveys within the first two weeks of the survey launch, some timing limits were reduced so that tourists could navigate the survey more quickly. However, no questions were changed, added or removed; thus, any complete surveys collected during this time were incorporated into the final analysis.

Respondents accessed the survey through QR codes or a web address link. QR codes were displayed on posters placed in areas with high tourist traffic (such as the domestic airport, dive centre, restaurant, and cafes) and on business cards which were handed out to tourists

opportunistically by the staff of Maldives Manta Conservation Programme (MMCP) or Pelagic Divers Fuvahmulah (PDF). Web address links were sent to tourists through email correspondence. The Pelagic Divers Fuvahmulah dive centre was the primary location used to promote the survey. Both PDF and MMCP staff were briefed on how to introduce the survey to tourists and were instructed to inform tourists that participation was voluntary and anonymous. If tourists were approached after a dive, respondents usually completed the survey immediately while the staff was available to answer questions. If tourists were approached before a dive, respondents usually collected the business card, choosing to complete the survey later. Surveys took approximately 15 minutes to complete. The target population included foreign tourists and tourists who are citizens or residents of the Maldives. Tourists were required to be 18 or older to participate in the study. Sampling took place exclusively on Fuvahmulah, and the survey was written in English, the most used language to communicate cross-culturally in the Maldives (Meierkord, 2018). The survey remained open from January 2023 to February 2024.

3.3.4 Statistical analysis

Responses were analyzed using R version 4.2.2 (R Core Team, 2022). Datasets were analyzed to differentiate between genuine and protest zero bids (Bateman et al., 2002). We identified one protest bid ($n = 1$) within our dataset in which the respondent specified that they felt the money should come from other places and would likely not be spent responsibly on conservation. Although protest bids may introduce unwanted noise in analysis, we determined the introduced noise was minimal and we, therefore, did not filter this respondent out of our final analysis (Johnston et al., 2017). The respondent seemed to clearly understand the questions presented and based on political views, opted to enter a zero bid. Subsequently answered questions suggested that the protest response was not pervasive or influential on the remainder of

the survey. Furthermore, sensitivity analysis revealed that the protest bid showed little impact on results. The protest response and true zero bid ($n = 2$) were incorporate in our final analysis. The average willingness to pay was calculated from all respondents who answered the trap question correctly ($n = 93$).

To investigate the intricacies of accepted entrance fee prices, we used the van Westendorp Price Sensitivity Meter (Van Westendorp, 1976). This method provides an estimation of consumer price preferences for products of a unknown value and was recently used to determine the willingness of visitors to South Africa to pay additional fees to replace revenues gained by trophy hunting (Moorhouse et al., 2023). The van Westendorp methodology involves the description of a novel product after which respondents are asked to state the values at which they deem the product to be “too cheap” and “too expensive” (Van Westendorp, 1976). For the current study, we presented the questions as a request to identify the price at which the fee would be too low to make a meaningful contribution to marine conservation and the price at which the fee would be so expensive that it could deter future trips. The resulting data was visually inspected to depict the cumulative distribution functions and identify the optimal price point for the described product (Van Westendorp, 1976). Responses were removed ($n = 10$) if stated payment values for the entrance fee fell outside the price range stated in the van Westendorp analysis.

The proportion of funding dedicated to each initiative was analyzed using beta regression mixed models in the package ‘glmmTMB’ (Brooks et al., 2022). Models included the initiative type and the random effect of respondent ID as explanatory variables. The proportion of funding stated (range from 0-1) was the response variable. Since response variables of beta regression need to be bound between 0 and 1, a value of 0.001 was added and subtracted from the lower and upper bound, respectively. Planned contrasts were conducted for *post hoc* analysis of differences

between the initiative types. The effects of demographics and dive tourist preference and experience on willingness to pay were explored using nonparametric Kruskal-Wallis tests (KW; $\alpha = 0.05$) from the package ‘stats’ considering we had small sample sizes and non-normal distribution of responses (R Core Team, 2022). Although non-parametric analysis is robust in comparing groups of different sample sizes, we excluded groups from comparison in the KW tests if they included four or less respondents to further limit the impact of small sample size on results. If KW was significant (≤ 0.05), a *post hoc* Conover-Iman test from the R package ‘conover.test’ was conducted for multiple comparisons between groups (Dinno, 2024).

3.4 Results

3.4.1 Sample characteristics

In total, 94 completed surveys were collected from January 2023 to February 2024 primarily from foreign scuba divers, who held high pro-environmental attitudes and demonstrated concern regarding elasmobranch population declines. Over 90% of respondents were foreign visitors (from countries outside the Maldives; $n = 86$). Due to the limited number of responses from Maldivian nationals ($n=8$), we combined responses into one tourist group for analysis. Responses from Maldivian nationals ($n = 8$) were combined with responses from international visitors ($n = 86$) after inspecting the distributions of WTP within the groups, and after inspecting subsequent questions for significant outliers. Respondents ranged in age from 21-24 to 65+, although most were between 25-54 (Table 3.1). Male and female respondents were roughly equally represented, and income levels were mixed. The NEP survey categorized most respondents as having moderate ecological worldviews ($n = 74$; Table 3.1, Figure B1). Many respondents were highly educated, with 73% ($n = 68$) achieving a minimum of a bachelor’s or

associate's degree (Table 3.1). Many indicated they previously contributed financially to a non-profit organization (74%; $n = 69$). Furthermore, those who had previously donated to a non-profit organization most specifically contributed to wildlife or ecosystem protection (79%, $n = 55$; Table 3.1). Nearly all respondents reported some previous interaction with sharks and rays ($n = 92$; Table 3.2), knew of the current population declines of sharks and rays ($n = 91$), and expressed concern about these declines ($n = 66$; Table 3.2).

We identified all visitors as dive tourists, individuals primarily engaged in dive tourism-related activities such as snorkelling, freediving, or scuba diving. One respondent, however, indicated that neither scuba diving, freediving, nor snorkelling was their primary reason to visit Fuvahmulah and instead listed “ocean conservation” as their primary reason. Although we suspect this individual was also a visitor engaged in dive tourism (concluded from answers to questions related to species encounters), we excluded this respondent from our analyses specifically relevant to dive tourists because we could not present follow-up questions to them. Additionally, we removed another respondent ($n = 1$) from our full analysis as they answered the trap question incorrectly.

Dive tourists ($n = 92$) were most often scuba divers ($n = 84$; Table 3.3). Furthermore, most scuba divers indicated they were advanced or professional ($n = 67$). Seven respondents indicated that freediving was their primary activity with mixed skill levels, and one respondent was engaged in snorkelling activities at a beginner level (Table 3.3). We classified dive tourists as committed, or casual based on the frequency of dive trips and reported skill level in their primary activity (Table B1). Most dive tourists were committed to undertaking more frequent trips at higher skill levels ($n = 80$, 87%), and 32% ($n = 29$) were returning dive tourists indicating they had previously visited Fuvahmulah before their current trip at least once (Table 3.3). Nearly

all dive tourists indicated that their trip was motivated by the potential encounter of certain marine organisms (93%, n = 86; Table 3.3).

3.4.2 Willingness to pay

Of all respondents, 94% (n = 87) indicated that they would be willing to pay a one-time “Reserve” entry fee to Fuvahmulah Atoll Biosphere Reserve to support conservation initiatives on the island. Of the three respondents who selected a 0 bid, two were identified as true zeros, indicating, “I feel I cannot pay more to contribute to these conservation initiatives.” The final zero bid was recognized as a protest bid indicating “I don’t believe the money will be spent responsibly on conservation initiatives” and “I feel the money for these initiatives should come from other places.” The protest bid did not significantly affect the distribution of payment values, and did not seem to affect answers provided to subsequent questions; therefore, all responses (n = 93) were included in the willingness to pay analysis.

The average fee respondents reported being willing to pay for reserve entry was US\$58.17 (range = US\$0-200; Figure 3.2a). The van Westendorp Price Sensitivity Meter supported these results and found the optimal price to be US\$50 with suitable prices identified between US\$25-100 (Figure 3.2b). Of those who stated they would be willing to pay a reserve entry fee, most believed this fee should be charged to all visiting tourists (58%, n = 48), with some respondents specifying that Maldivian and work permit holders should be charged less (n = 3; Figure B2).

Of those who were willing to pay an entrance fee to Fuvahmulah Atoll, respondents allocated, on average, 21-29% of the fee across the initiatives; MPA management, waste management, community education and marine research facilities (Figure 3.3). The proportion of

funding allocated to MPA, and waste management was significantly higher than the funding allocated to community education and marine research facilities (Figure 3.3; Table 3.4).

3.4.3 Factors affecting WTP

We found limited evidence of the impact of demographics on WTP. Age, gender, and education did not affect the value of WTP (Table 6). Although we found a significant effect of income on WTP value ($\chi^2 = 16.64$, $df = 7$ $p = 0.02$; Table 3.5), there were no observed patterns between the tested income categories, and corrected *p*-values for *post hoc* comparisons were insignificant (Table 3.6).

Environmental attitudes and donation history impacted the amount visitors were willing to pay for the entrance fee. There was a general trend of increasing WTP value with stronger ecological worldviews (as measured by the NEP scale); however, only respondents with a strong ecological worldview had significantly higher WTP values than those with an ambiguous worldview ($p = 0.036$; Table 3.6, Figure 3.4c). Respondents with no donation history reported a wide range of WTP values, which were significantly higher than the WTP values reported by respondents donating to other causes (apart from ecosystem or wildlife protection; $p = 0.045$; Table 3.6; Figure 3.4a). Additionally, respondents who donated specifically to non-profits for the protection of ecosystems or wildlife had a higher willingness to pay values than those who donated elsewhere ($p = 0.011$; Table 3.6, Figure 3.4a).

Many respondents were aware of the current global declines of shark and ray populations ($n = 91$), and all expressed some level of concern. Concern level significantly impacted WTP values ($\chi^2 = 8.16$, $df = 2$, $p = 0.017$; Table 3.5). Generally, WTP values increased with increasing concern (Figure 5b). Those who indicated they were extremely concerned had significantly

higher WTP values than those who were only moderately concerned ($p = 0.0073$; Table 3.6; Figure 3.4b).

Respondents' previous experience with sharks and rays and their experience in Fuvahmulah Atoll impacted WTP. Tourists reporting previous encounters with sharks and rays while scuba diving, snorkelling or freediving had higher WTP values than those who did not report previous encounters ($\chi^2 = 6.88$, $df = 1$, $p = 0.0087$; Table 3.5). Additionally, those who reported watching movies or documentaries about sharks and rays had significantly higher WTP than those who hadn't watched films ($\chi^2 = 3.81$, $df = 1$, $p = 0.051$; Table 3.5). Other previous interactions, including trips focusing on encounters, research activities, and encountering sharks and rays in an aquarium setting, showed no significant impact on WTP (Table 3.5). Dive tourists who visited Fuvahmulah in the past did not have significantly different WTP values than those who indicated they were first-time visitors ($\chi^2 = 0.071$, $df = 1$, $p = 0.79$; Table 3.5). Those who were considered committed dive tourists (undergoing more frequent dive tourist trips and maintaining high skill levels) showed significantly higher WTP values compared to those who were casual dive tourists ($\chi^2 = 7.14$, $df = 1$, $p = 0.0075$; Table 3.5; Figure 3.5b). While many dive tourists were motivated to visit Fuvahmulah to encounter specific species ($n = 86$; Table 3.3, Figure B3), WTP was not significantly affected by the primary species selected for motivating visitation to Fuvahmulah ($\chi^2 = 3.37$, $df = 5$, $p = 0.64$; Table 3.5). However, the reported encounters with specific megafauna within Fuvahmulah Atoll did affect WTP values. Specifically, WTP was significantly higher for dive tourists reporting encounters of tiger sharks ($\chi^2 = 6.68$, $df = 1$, $p = 0.0097$; Table 3.5) and thresher sharks ($\chi^2 = 6.28$, $df = 1$, $p = 0.012$; Table 3.5, Figure 3.5c,d) in Fuvahmulah. Tiger and pelagic thresher sharks were the most frequently selected as the primary motivator for visiting Fuvahmulah and the most frequently encountered

species (Figure B3). However, encountering the top motivating species had nonsignificant impacts on WTP ($\chi^2 = 3.33$, $df = 1$, $p = 0.068$; Table 3.5). No other encounters in Fuvahmulah Atoll affected WTP values (Table 3.5).

3.5 Discussion

Our survey results indicate that tourists are willing to contribute to marine conservation financing through park entry fees in Fuvahmulah Atoll. The average value that tourists were willing to pay was US\$58.17, and the van Westendorp Price Sensitivity Meter revealed that fees between US\$25 and US\$100 would be considered appropriate by most tourists. The recognized need for increased conservation measures on the island was evident in the analysis of feedback provided by respondents at the end of the survey. One respondent stated, *“Urgent decision-making must be done as soon as possible in order to protect the marine life in Fuvahmulah.”* Another respondent alluded to the risks associated with unregulated tourism, stating, *“Fuvahmulah is a heaven on earth that should be persevered and managed in such a way that tourism doesn’t ruin its natural wild heart. Even if it meant limiting the [number] of tourists it hosts at any given moment.”*

We found that tourists preferentially support allocating funds to marine protected area management and waste management over community education and research facilities. Previous research has identified a link between time spent within an environment and the willingness to pay for its conservation (Schuhmann et al., 2023). Dive tourists are generally willing to pay entrance fees provided that the revenue gained is used for conservation improvement instead of generating general revenue for government bodies (Peters & Hawkins, 2009). While other studies have identified the willingness of visitors to increase donations to support community education specifically (Murphy et al., 2018), respondents in the current study can likely identify

a direct link between MPA management, waste management, and marine conservation. Additionally, Pelagic Divers Fuvahmulah, the local dive centre where most responses were collected, has supported installing built-in water filtration systems on the island to reduce plastic accumulation. Therefore, guests of the dive centre may be more aware of waste management issues and more inclined to support these efforts. The connection between marine conservation and community education may be more nuanced, and marine research facilities may not inherently be linked to conservation. Our findings suggest that an increased awareness surrounding specific initiatives and highlighting direct connections to marine conservation may increasingly support implementing a multi-use management plan.

Our results suggest that WTP depends on the entrance fee used to support marine conservation. However, with increased government decentralization, revenue gained by charging entrance fees represents a tempting resource for local authorities in developing countries (Emerton et al., 2006; Peters & Hawkins, 2009). While we recognize that the initiatives presented in the current study are not an exhaustive list of those possible, the WTP values reported here were collected after highlighting the various conservation initiatives in Fuvahmulah Atoll that the fee could support. Respondents answered survey questions while assuming that their fee would be going towards these initiatives, at least in part. Previous studies have identified a link between revenue use and WTP. Agreements to fee implementation within marine parks in Malaysia and Indonesia depended upon revenue being used for marine park management, and higher fees were accepted by respondents if how the revenue was used remained transparent (Walpole et al., 2001; Yeo, 2005). The only protest bid identified in the study specified that they felt the money would not be spent responsibly on nature, further highlighting the importance of transparency. Ensuring revenues are channelled to island

conservation while maintaining expenditure transparency would likely positively impact long-term visitor WTP.

Most tourists indicated that entrance fees should be charged to all tourists visiting Fuvahmulah Atoll and not specifically directed to those accessing protected areas. This finding is interesting, considering all tourists were involved with dive tourism. It may be assumed that travel of any kind would inherently impact the marine ecosystems since the island is built upon coral reefs. With the entire island declared a UNESCO Biosphere Reserve (BR), fees to visit the island for any reason may be justified. A fee structure is typically site-dependent when comparing the global network of BRs, and there is no unified approach (Peters & Hawkins, 2009). Many sites implement fees to access specific areas within the BR or to partake in particular activities (e.g., hiking or scuba diving). The Galápagos Biosphere Reserve does, however, charge visitors a general entrance fee to support conservation efforts (Benitez, 2001). A similar approach to that of the Galápagos may be appropriate at Fuvahmulah Atoll; however, we only captured the WTP and associated preferences of dive tourists, who are mostly foreigners. Many developing countries differentially charge foreign tourists and residents or visa holders (Apollo, 2014; Peters & Hawkins, 2009). Additional work should aim to assess the WTP of visitors not participating in dive tourism activities and Maldivian visitors.

While we found that nearly all tourists are willing to pay to contribute to conservation initiatives on the island, the amount depended on various factors, including environmental attitudes, and donation history. Tourists' WTP were widespread across demographics, with no significant difference found across income levels, gender, education, or age. Environmental attitudes, however, did impact the amount tourists were willing to contribute towards entrance fees in multiple ways. Stronger ecological worldviews measured through the NEP scale and

increased concern for declining shark and ray populations were associated with higher WTP. Other studies have identified a similar relationship between WTP and environmental attitudes. Visitors to the Galapagos marine park, considered “pro-environmental” based on the NEP scale, were willing to pay more for seafood with lower associated bycatch (Tanner et al., 2021). Similarly, Booth et al. (2002) found that tourists with stronger pro-environmental attitudes were willing to pay higher fees for shark conservation in Indonesia.

We found that donation history positively impacted WTP values. Respondents who reported specifically donating to charities which protect wildlife or ecosystems were associated with higher WTP than those who donated elsewhere. Previous research reported the positive impact of donation history on the intention to donate money to recover threatened shark species (Cárdenas & Lew, 2016). In contrast, Lewis et al. (2018) found no significant impact of previous donation behaviour on conservation and community. Here, we found that the specific cause to which respondents donated was an important determinant when assessing the impact of donation history on WTP.

We found that dive tourist commitment (i.e., the skill level maintained and frequency of dive trips) and previous interactions with sharks and rays impacted the amount visitors were willing to pay. More experienced divers tend to have higher ecological awareness which can translate to higher WTP (Dearden et al., 2006; Anderson & Loomis, 2011; Malpica-Cruz et al., 2017). Committed dive tourists, who take more frequent dive tourism trips and maintain more advanced skill levels, were associated with higher WTP. Similarly, Malpica-Cruz et al. (2017) found that committed divers, who possessed more ecological knowledge and had higher engagement levels with diving, were willing to pay higher fees for marine conservation. In addition to dive tourist commitment, visitors who reported previously encountering sharks and

rays were associated with higher WTP values. Additionally, those who reported watching movies or documentaries about sharks or rays had significantly higher WTP. Other previous interactions showed no impact on WTP, including participating in trips focusing on shark and ray encounters and viewing sharks and rays in aquarium settings, suggesting that, while respondents have been willing to pay for trips in the hopes of encountering sharks and rays, it's specifically successful trips which affect the amount that tourists are willing to contribute to Fuvahmulah conservation. Marine wildlife tours can promote pro-environmental attitudes held by tourists, and studies have shown that encounters can promote higher WTP if the funds aid wildlife protection (Tisdell & Wilson, 2001). Furthermore, shark encounters in the wild have positively impacted the willingness to pay for shark conservation in other studies (Booth et al., 2022). Since most tourists in the current study were motivated to travel to Fuvahmulah for shark/ray encounters and were committed to dive tourism, it's likely that those who have previously encountered sharks/rays partake in these excursions more frequently and may be more invested in marine conservation.

Although respondents reported encounters with several megafauna species, those reporting encounters with tiger sharks or pelagic threshers at Fuvahmulah Atoll were associated with higher WTP values. Charismatic species, which are associated with particular habitats or geographic locations, represent opportunities to act as flagship species to encourage more general conservation action (Walpole & Leader-Williams, 2002; Kontoleon & Swanson, 2003; Colléony et al., 2017). Although other charismatic species were encountered, no other encounters demonstrated an impact on WTP. The frequency of encounters has been identified as an important factor in determining the effect of megafauna interactions on WTP (Batel et al., 2014). It's likely that while other species were encountered and may contribute to the attractiveness of

Fuvahmulah Atoll as a dive destination, tiger sharks and pelagic threshers were the most consistently encountered and, therefore, have a stronger impact on WTP.

The effect of tiger sharks and pelagic thresher encounters on WTP is likely a result of the combination of these species being the top motivators for Fuvahmulah trips and the high frequency of tiger shark and thresher shark encounters. In Fuvahmulah, tiger sharks are encountered on a regular basis at the Tiger Harbour dive site where fish scraps are used to attract sharks to the mouth of the harbour (Araujo et al., 2024). Pelagic threshers are also frequently encountered at pelagic thresher shark cleaning stations, which local dive operators have identified. Cleaning stations are ecologically significant sites which pelagic threshers routinely visit to have bacteria and parasites removed through the symbiotic relationship they hold with cleaner fish (Oliver et al., 2011). Furthermore, this behaviour is sensitive to dive tourism activities. Dive tourists visiting manta ray (*Mobula alfredi*) cleaning stations in Australia negatively impacted the amount of time manta rays spent actively cleaning (Venables, 2013). Similarly, scuba divers in Philippines interrupted thresher shark cleaning behaviour at a coastal seamount (Oliver et al., 2011). The potential dependency on the frequency of encounters suggests that WTP may be negatively impacted if megafauna visitation is disrupted or becomes less frequent as a result of tourism activities, further highlighting the need for effective marine conservation measures.

Tourists to Fuvahmulah Atoll provide an opportunity for increased marine conservation efforts through their willingness to pay a one-time “Reserve” entrance fee. As a remote destination boasting abundant and diverse marine life, Fuvahmulah Atoll attracts highly trained and committed dive tourists. Dive tourists often possess foundational ecological knowledge related to marine ecosystems, and by spending time underwater, many divers have witnessed

changes as human influence continues to shape the underwater ecosystems. Here, we demonstrated that visitors to Fuvahmulah Atoll are concerned about declining shark and ray populations and uphold strong environmental values that positively influence WTP values. Additionally, we identified the dependent nature of tourism to Fuvahmulah on specific species encounters by documenting a high number of visitors motivated by encounters and the positive impact of tiger shark and pelagic thresher encounters on WTP. When channelled to marine conservation, funds generated by entrance fees can increase the protection of species and habitats on which tourism to Fuvahmulah depends. Increasing marine conservation efforts on Fuvahmulah Atoll is more achievable through tourism and could also ensure the tourism industry's sustainability for the years to come.

3.6 Tables and Figures

Table 3.1. Demographics of visitors to Fuvahmulah Atoll (n = 93). Percentage of total respondents in each category is included in parenthesis.

Variable	Number of respondents
Age	
Under 21	0 (0.00%)
21-24	3 (3.22%)
25-34	37 (39.78%)
35-44	32 (34.41%)
45-54	15 (16.13%)
55-64	4 (4.30%)
65+	1 (1.08%)
Prefer not to say	1 (1.08%)
Gender	
Female	44 (52.69%)
Male	49 (47.31%)
Prefer to identify in another way	0 (0.00%)
Income (USD)	
< 20,000	8 (8.60%)
20,000-39,999	14 (15.05%)
40,000-59,999	12 (12.90%)
60,000-79,999	12 (12.90%)
80,000-99,999	10 (10.76%)
100,000-149,999	8 (8.60%)
150,000-199,999	9 (9.68%)
200,000-499,999	6 (6.45%)
> or equal to 500,000	1 (1.08%)
Prefer not to say	13 (13.98%)
NEP category	
Strong social	0 (0.00%)
Moderate social	1 (1.08%)
Ambiguous	13 (13.98%)
Moderate ecological	74 (79.57%)
Strong ecological	5 (5.37%)
Education	
Elementary/middle school graduate (gr 8-10)	0 (0.00%)
High school graduate (gr 9-12)	12 (12.90%)
Some post-secondary	12 (12.90%)
Bachelor's degree/associate's degree	41 (44.09%)
Doctorate/master's/professional degree	27 (29.03%)
I'd rather not say	1 (1.08%)
Donation history	
No donation history	24 (25.81%)
Donated in the past	14 (15.05%)
Donated in the past specifically for wildlife/ecosystem protection	55 (59.14%)

Table 3.2. Fuvahmulah Atoll respondents' previous interactions and knowledge of sharks and rays (n = 93). The percentage of total respondents in each category is included in parentheses.

Variable	Number of respondents
Previous interactions^a	
Research	14 (15.05%)
Encountered while scuba, snorkelling	77 (82.80%)
Participated in trips focused on encounters	68 (73.12%)
Watched movies or documentaries	60 (64.52%)
Visited in aquarium	38 (40.86%)
Supported campaigns/NGOs	2 (2.15%)
No previous interaction	1 (1.08%)
Awareness of shark/ray population declines	
Yes	91 (97.84%)
No	1 (1.08%)
Unsure	1 (1.08%)
Level of concern for shark/ray populations	
Not concerned	0 (0.00%)
Slightly Concerned	3 (3.23%)
Moderately Concerned	12 (12.90%)
Very Concerned	12 (12.90%)
Extremely Concerned	66 (70.97%)

^avalues exceed 100% for previous interactions- respondents could select multiple answers

Table 3.3. Dive tourist experience and motivations in Fuvahmulah Atoll (n = 92). The percentage of total respondents in each category is included in parentheses.

Variable	Number of respondents
Primary dive tourism activity and skill level	
Snorkelling (total)	1 (1.09%)
Beginner	1 (100%)
Intermediate	0 (0.00%)
Advanced	0 (0.00%)
Professional	0 (0.00%)
Freediving (total)	7 (7.61%)
Beginner	0 (0.00%)
Intermediate	3 (42.86%)
Advanced	2 (28.57%)
Professional	2 (28.57%)
Scuba diving (total)	84 (91.30%)
Beginner	1 (1.19%)
Intermediate	16 (19.05%)
Advanced	46 (54.76%)
Professional	21 (25.00%)
Previous trips to Fuvahmulah for diving	
1x	17 (18.48%)
2x	3 (3.26%)
3-5x	7 (7.61%)
> 5x	2 (2.17%)
Never	63 (68.48%)
Diver commitment level	
Casual	12 (13.04%)
Committed	80 (86.96%)
Trip motivated by marine megafauna encounters	
Yes	86 (93.48%)
No	6 (6.52%)
Encountered top motivating species^a	
Yes	70 (81.40%)
No	16 (18.60%)

^aOnly included those who indicated their trip was motivated by an encounter with specific organisms (n =

86)

Table 3.4. Model estimates and p-values for the fixed effects of the beta regression model explaining the proportion of funding. Response ID was additionally included as a random variable. Asterisks and planned *post hoc* contrasts shaded green indicate significant differences between initiatives.

Initiative (fixed effect) ^a	Estimate	P-value ^b
MPA: Edu	0.28	0.016*
Res: Edu	-0.24	0.044*
Waste: Edu	0.20	0.087*
MPA: Res	0.52	1.3x10 ⁻⁵ ***
MPA: Waste	0.08	0.48
Res: Waste	-0.44	0.00023***

^aAbbreviations for proposed initiatives; MPA – marine protected areas management, Edu – community education, Res – marine research facilities, Waste – waste management.

^bNumber of asterisks represents significance level where * indicates $p \leq 0.05$, ** indicates $p \leq 0.01$, and *** indicates $p \leq 0.001$

Table 3.5. Non-parametric ANOVA results (Kruskal-Wallis test).

Variable^a	df	χ^2	P -value
Sociodemographic			
Age	2	0.066	0.97
Gender	1	1.58	0.21
Income	7	16.64	0.020*
Worldview (NEP)	2	6.06	0.048*
Education	3	3.10	0.38
Donation history	2	7.27	0.026*
Concern for population declines			
Moderately concerned, very concerned and highly concerned	2	8.16	0.017*
Previous interaction			
Encountered	1	6.88	0.0087**
Trips	1	1.72	0.19
Research	1	0.0058	0.94
Films	1	3.81	0.051*
Aquarium	1	0.27	0.61
Diver experience and motivations			
Repeat visitor	1	0.071	0.79
Commitment	1	7.14	0.0075**
Top motivating species ^c	5	3.37	0.64
Tiger shark encounter	1	6.68	0.0097**
Pelagic thresher encounter	1	6.28	0.012**
Hammerhead encounter	1	1.87	0.17
Manta ray encounter	1	0.64	0.42
Whaleshark encounter	1	0.74	0.39
Cetacean encounter	1	0.93	0.33
Encountered top motivating species ^c	1	3.33	0.068

^aOnly tested groups with more than four responses (refer to Tables 3.1-3.3)

^bNumber of asterisks represents significance level where * indicates $p \leq 0.05$, ** indicates $p \leq 0.01$, and *** indicates $p \leq 0.001$

^cUsed only responses from dive tourists who indicated their trip was motivated by encountering certain species (n = 86)

Table 3.6. Conover-Iman *post hoc* pairwise comparisons with Bonferroni correction for significant effects of KW tests where more than two groups are compared.

Variable ^a	t	p-value	Adj. p-value ^b
Income (USD)			
< 20,000 – 20,000: 39,999	1.50	0.069	1.00
< 20,000 – 40,000: 59,999	-1.02	0.16	1.00
< 20,000 – 60,000: 79,999	-0.55	0.29	1.00
< 20,000 – 80,000: 99,999	0.36	0.36	1.00
< 20,000 – 100,000: 149,999	1.85	0.03	0.97
< 20,000 – 150,000: 199,999	-1.00	0.16	1.00
< 20,000 – 200,000: 499,999	-0.60	0.27	1.00
20,000: 39,999 – 40,000: 59,999	-2.88	0.0027	0.07
20,000: 39,999 – 60,000: 79,999	-2.32	0.011	0.32
20,000: 39,999 – 80,000: 99,999	-1.19	0.12	1.00
20,000: 39,999 – 100,000: 149,999	0.58	0.28	1.00
20,000: 39,999 – 150,000: 199,999	-2.69	0.0045	0.12
20,000: 39,999 – 200,000: 499,999	-2.03	0.023	0.64
40,000: 59,999 – 60,000: 79,999	0.53	0.30	1.00
40,000: 59,999 – 80,000: 99,999	1.49	0.070	1.00
40,000: 59,999 – 100,000: 149,999	3.04	0.0016	0.05
40,000: 59,999 – 150,000: 199,999	-0.04	0.48	1.00
40,000: 59,999 – 200,000: 499,999	0.28	0.39	1.00
60,000: 79,999 – 80,000: 99,999	0.98	0.16	1.00
60,000: 79,999 – 100,000: 149,999	2.57	0.0061	0.17
60,000: 79,999 – 150,000: 199,999	-0.53	0.30	1.00
60,000: 79,999 – 200,000: 499,999	-0.15	0.44	1.00
80,000: 99,999 – 100,000: 149,999	1.58	0.059	1.00
80,000: 99,999 – 150,000: 199,999	-1.43	0.079	1.00
80,000: 99,999 – 200,000: 499,999	-0.97	0.17	1.00
100,000: 149,999 – 150,000: 199,999	-2.90	0.0025	0.07
100,000: 149,999 – 200,000: 499,999	-2.31	0.012	0.33
150,000: 199,999 – 200,000: 499,999	0.30	0.38	1.00
NEP category			
Ambiguous – moderate ecological	-2.02	0.023	0.069
Ambiguous – strong ecological	-2.30	0.012	0.036*
Moderate ecological – strong ecological	-1.30	0.099	0.30
Donations for conservation			
No donation history – previously donated to other cause	2.20	0.015	0.045*
No donation history – donated for ecosystem/wildlife protection	-0.34	0.37	1.00
Donated for ecosystem wildlife protection – previously donated to other cause	2.76	0.0035	0.011**
Concern for population declines			
Moderately concerned - very concerned	-1.39	0.085	0.25
Moderately concerned - extremely concerned	-2.89	0.0024	0.0073**
Very concerned - extremely concerned	-1.089	0.14	0.42

^aOnly included groups with more than four responses for pairwise comparisons (refer to Tables 1-3)

^bNumber of asterisks represents significance level where * indicates $p \leq 0.05$, ** indicates $p \leq 0.01$, and *** indicates $p \leq 0.001$

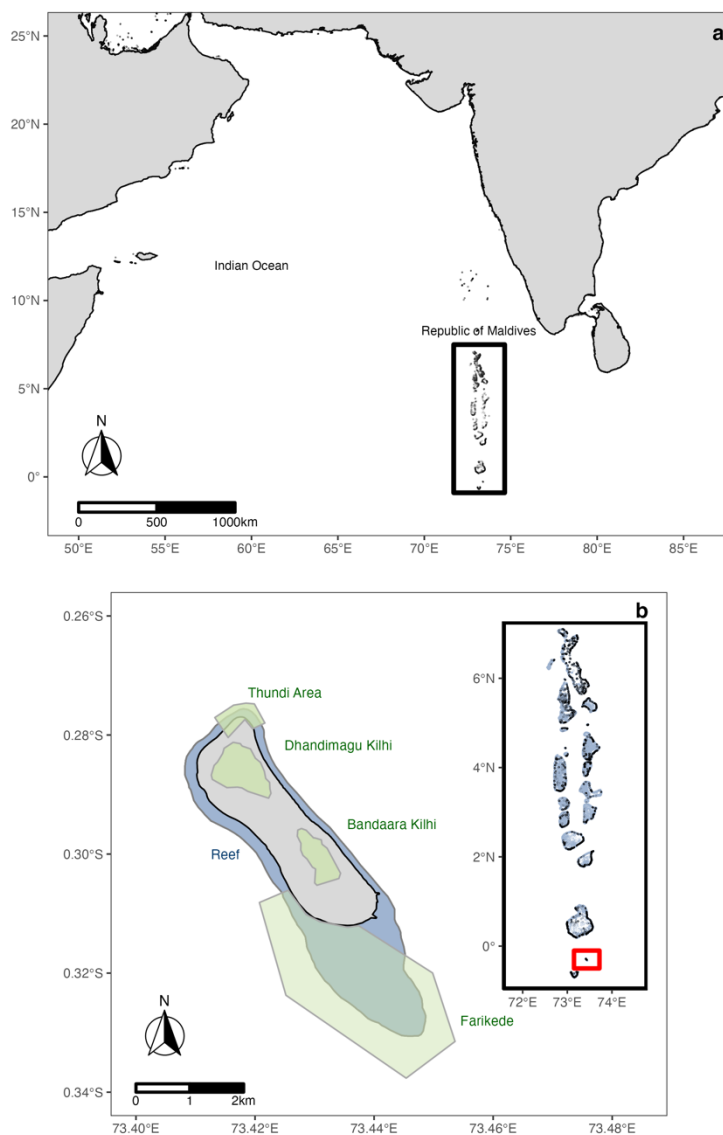


Figure 3.1. Map of the Republic of Maldives within the Indian Ocean (a) and Fuvahmulah Atoll (b). Designated protected areas are displayed and include Thundi Area, Dhandimagu Kilhi, Bandaara Kilhi and Farikede. The red box displays the position of Fuvahmulah Atoll within the Maldives.

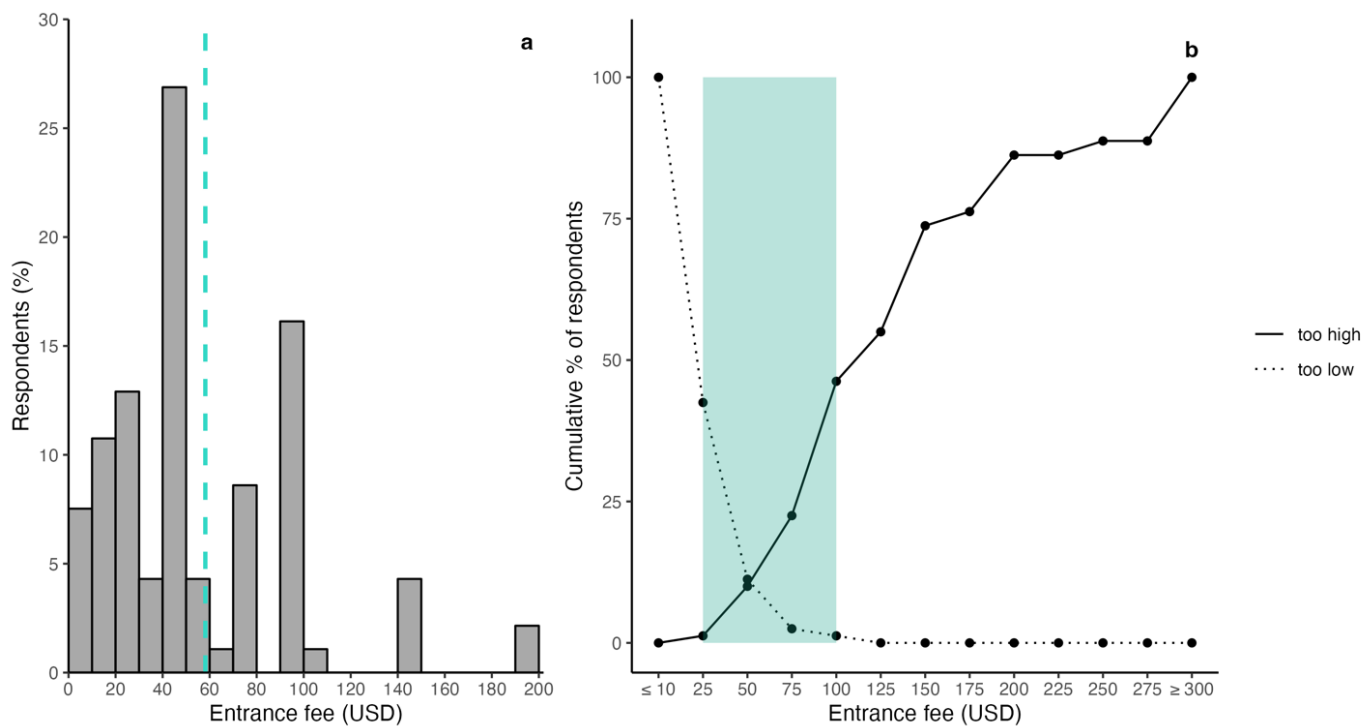


Figure 3.2. The distribution of Fuvahmulah Atoll “Reserve” entrance fees stated by respondents (a; $n = 93$) and van Westendorp price sensitivity analysis (b). The dashed line (a) indicates an average entrance fee of US\$58.17. The green shaded area (b) indicates the interval in which less than 50% of respondents think the fee is too expensive, deterring future trips, and less than 50% of respondents feel the fee is too cheap to make an impact on marine conservation in Fuvahmulah. The intersection of the lines “too high” and “too low” shows that the optimal price point lies at US\$50 (b).

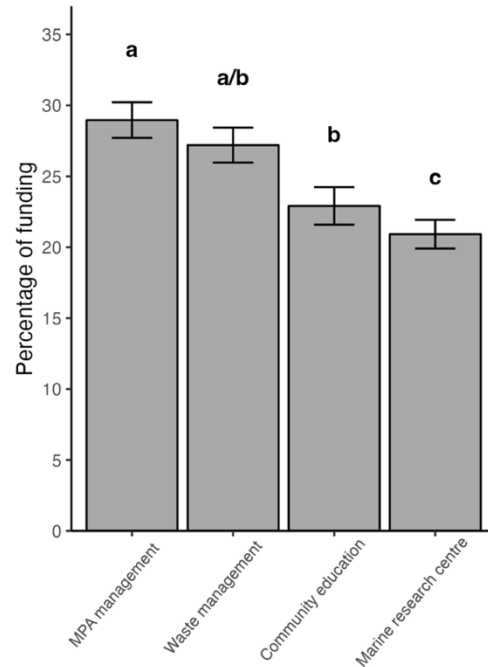


Figure 3.3. Percentage of funding allocated to MPA (marine protected area) management and waste management, community education and marine research facilities by respondents who indicated a positive willingness to pay for Fuvahmulah Atoll entrance fees ($n = 90$). Error bars represent standard error, and letters denote significant differences from the beta regression model.

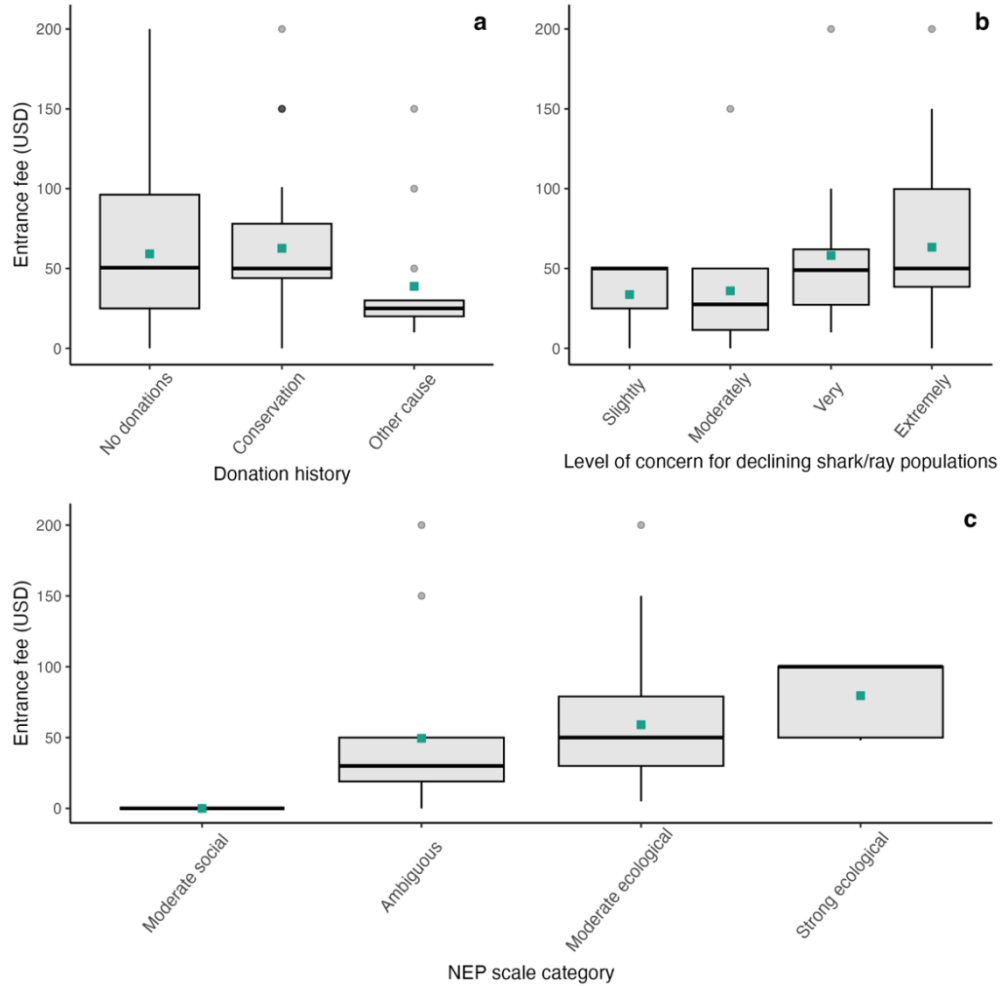


Figure 3.4. Variation in entrance fees (USD) associated with (a) previous donation behaviour, (b) concern for declining shark populations, and (c) the NEP scale. Categories that were not selected by respondents were not included; “no level of concern” towards declining shark and ray populations, and “strong social” NEP scale category. Coloured squares within boxplots represent the mean, and points above boxplots represent outliers.

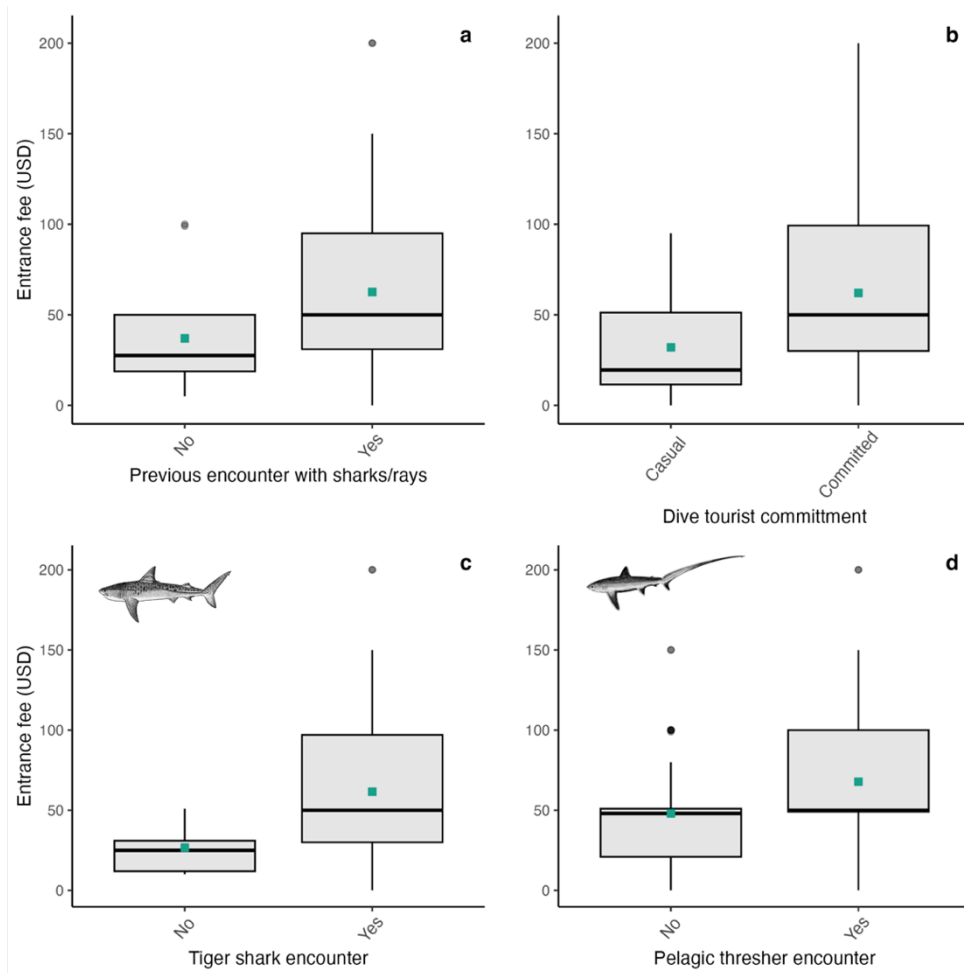


Figure 3.5. Variation in entrance fees (USD) associated with (a) previous shark and ray encounters, (b) dive tourist commitment, and (c,d) encounters in Fuvahmulah Atoll with tiger sharks (*Galeocerdo cuvier*) and pelagic threshers (*Alopias pelagicus*). Coloured squares within boxplots represent means and points represent outliers.

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Appendices

Appendix A: Supplemental information or Chapter 2

Table A1. Certainty scores assigned to each captured in timelapse footage.

Certainty Score	Description
0	No distinguishing features are visible, species ID is listed as “Unknown Shark” or “Unknown Ray”
1	Few distinguishing features are visible, correct ID is likely but not certain
2	Some distinguishing features are visible, reasonable confidence in ID
3	Many distinguishing features are visible, high confidence in ID

Table A2. Top models for **daily** occurrence, relative abundance, and sub-hourly FO. Models that were run together using the hurdle model approach are indicated in red text. Sub-daily FO is measured by the proportion of 1-hour intervals within a day that species were sighted on.

Species	Response Variable	Top Model	Distribution	Dispersion Coefficient ^a
Whitetip Reef Shark	Occurrence	Null	Binomial Hurdle	
	Relative Abundance	Date + Site	Poisson Hurdle	P = 1.07 NB = 1.07
	Sub-daily FO	Date * Site	Quasibinomial	
Pelagic Thresher Shark	Occurrence	Site	Binomial Hurdle	
	Relative Abundance	Date + Site	Poisson Hurdle	P = 0.78 NB = 0.78
	Sub-daily FO	Date + Site	Quasibinomial	
Grey Reef Shark	Occurrence	Site	Binomial	
	Relative Abundance	Date + Site	Negative Binomial	P = 6.1 NB = 2.3
	Sub-daily FO	Date + Site	Quasibinomial	
Tiger Shark	Occurrence	Date + Site	Binomial	
	Relative Abundance	Date + Site	Poisson	P = 0.52 NB = 0.52
	Sub-daily FO	Date + Site	Quasibinomial	
Silvertip Shark	Occurrence	Null	Binomial Hurdle	
	Relative Abundance	Null	Negative Binomial Hurdle	P = 1.35 NB = 0.95
	Sub-daily FO	Date	Quasibinomial	

^aDispersion coefficients for Poisson (P) and negative binomial (NB) distributions

Table A3. Top model for **hourly** occurrence, relative abundance, and sub-hourly FO. Models that were run together using the hurdle model approach are indicated in red text. Sub-hourly FO is measured by the proportion of 10-minute intervals within an hour that species were sighted on.

Species	Response Variable	Top Model^a	Distribution	Dispersion Coefficient^b
Whitetip Reef Shark	Occurrence	Hour * Site	Binomial Hurdle	P = 1.08 NB = 1.02
	Relative Abundance	Hour * Site	Negative Binomial Hurdle	
	Sub-hourly FO	Hour * Site	Quasibinomial	
Pelagic Thresher Shark	Occurrence	<i>Hour + Site</i>	Binomial Hurdle	P = 1.097 NB = 1.097
	Relative Abundance	<i>Hour + Site</i>	Poisson Hurdle	
	Sub-hourly FO	<i>Hour + Site</i>	Quasibinomial	
Grey Reef Shark	Occurrence	Site	Binomial Hurdle	P = 1.90 NB = 1.17
	Relative Abundance	<i>Hour + Site</i>	Negative Binomial Hurdle	
	Sub-hourly FO	<i>Hour + Site</i>	Quasibinomial	
Tiger Shark	Occurrence	Hour * Site	Binomial Hurdle	P = 0.98 NB = 0.98
	Relative Abundance	Null	Poisson Hurdle	
	Sub-hourly FO	<i>Hour + Site</i>	Quasibinomial	
Silvertip Shark	Occurrence	<i>Hour</i>	Binomial Hurdle	P = 1.016 NB = 0.9845
	Relative Abundance	<i>Hour</i>	Poisson Hurdle	
	Sub-hourly FO	<i>Hour</i>	Quasibinomial	

^aHour italicized where 2nd order polynomial was significant

^bDispersion coefficients for poisson (P) and negative binomial (NB) distributions

Table A4. Model estimates and p-values for fixed effects included in the top models for **daily (left) and hourly (right)** occurrence (presence-absence). Planned *post hoc* contrasts are shaded yellow. Site comparisons include Hudhekede (HK), Kedevari (KV) and Farikede (FK).

Species	Fixed Effect	Estimate	P-value
Pelagic thresher	FK-HK	1.21	0.11
	KV-HK	1.82	0.0082
	KV-FK	0.61	0.47
Grey reef shark	FK-HK	3.39	0.027
	KV-HK	0.66	0.23
	KV-FK	-2.72	0.072
Tiger shark	FK-HK	5.18	0.0015
	KV-HK	1.07	0.093
	KV-FK	-4.11	0.0078
	Date	-0.025	0.0011

Species	Fixed Effect	Estimate	P-value
Whitetip reef shark	FK-HK	0.13	0.84
	KV-HK	-1.53	0.0077
	KV-FK	-1.63	4.54e-20
	Hour	-0.13	0.00089
	KV*Hour: HK*Hour	0.13	0.0079
	FK*Hour: HK*Hour	0.13	0.019
	KV*Hour: FK*Hour	0.0018	0.97
Pelagic thresher	FK-HK	1.77	4.05e-12
	KV-HK	2.29	2.26e-22
	KV-FK	0.52	0.0045
	poly(Hour,2)1	-23.22	2.46e-11
	poly(Hour,2)2	-36.14	2.87e-25
Grey reef shark	FK-HK	2.93	7.52e-33
	KV-HK	0.32	0.19
	KV-FK	-2.62	7.69e-41
Tiger shark	FK-HK	3.37	0.0011
	KV-HK	0.071	0.95
	KV-FK	-1.42	6.95e-11
	Hour	0.065	0.37
	FK*Hour: HK*Hour	-0.12	0.15
	KV*Hour: HK*Hour	0.040	0.64
	KV*Hour: FK*Hour	0.16	0.0086
Silvertip Shark	poly(Hour,2)1	1.46	0.68
	poly(Hour,2)2	-8.35	0.023

Table A5. Model estimates and p-values for fixed effects included in the top models for **daily (left) and hourly (right)** relative abundance (MaxN). Planned *post hoc* contrasts are shaded yellow. Site comparisons include Hudhekede (HK), Kedevari (KV) and Farikede (FK).

Species	Fixed Effect	Estimate	P-value
Whitetip reef shark	FK-HK	1.29	0.0032
	KV-HK	-0.071	0.88
	KV-FK	-1.36	4.29e-05
	Date	0.0076	0.025
Pelagic thresher	FK-HK	2.11	0.043
	KV-HK	2.37	0.018
	KV-FK	0.26	0.48
	Date	-0.0069	0.11
Grey reef shark	FK-HK	1.90	2.01e-06
	KV-HK	0.82	0.03
	KV-FK	-1.08	0.00018
	Date	0.0082	0.013
Tiger shark	FK-HK	1.12	0.0075
	KV-HK	0.42	0.29
	KV-FK	-0.71	0.027
	Date	-0.0097	0.019

Species	Fixed Effect	Estimate	P-value
Whitetip reef shark	FK-HK	-5.54	0.048
	KV-HK	-6.96	0.018
	KV-FK	-1.41	2.09e-05
	Hour	-0.89	0.025
	KV*Hour: HK*Hour	0.88	0.029
	FK*Hour: HK*Hour	0.88	0.026
	KV*Hour:FK*Hour	0.00095	0.99
Pelagic thresher	FK-HK	1.40	0.17
	KV-HK	2.23	0.026
	KV-FK	0.83	0.0048
	Poly(Hour, 2)1	-42.13	0.00018
	Poly(Hour, 2)2	-28.08	0.0016
Grey reef shark	FK-HK	3.14	7.36e-05
	KV-HK	3.26	6.49e-05
	KV-FK	0.12	0.69
	Poly(Hour, 2)1	-4.73	0.31
	Poly(Hour, 2)2	-15.15	0.0052
Silvertip shark	Poly(Hour, 2)1	33.51	0.0031
	Poly(Hour, 2)2	-20.75	0.015

Table A7. Frequency of occurrence (%) of elasmobranchs in images, hours, and days.

Site	Image	Hourly	Daily
Overall	3.11%	72.02%	95.24%
Farikede	5.31%	90.73%	100%
Kedevari	3.44%	66.74%	94.87%
Hudhekede	0.56%	46.62%	92.31%

Table A8. Results of permutational multivariate analysis of variance (PERMANOVA) *post hoc* pairwise comparisons examining the effects of site and study period category on community composition. Sub-daily FO is measured by the proportion of one-hour intervals in a day that species were sighted on each day at the sites. Note that the F values reflect the pseudo-F statistic, and the Bonferroni correction has been applied to p-values for *post hoc* comparisons.

	Site			Date category		
	Hudhekede vs Kedevari	Hudhekede vs Farikede	Kedevari vs Farikede	Early vs Mid	Early vs Late	Mid vs Late
Occurrence and relative abundance	F = 6.36 R ² = 0.10 p = 0.003	F = 23.33 R ² = 0.36 p = 0.003	F = 19.48 R ² = 0.26 p = 0.003	F = 4.57 R ² = 0.05 p = 0.004	F = 8.24 R ² = 0.11 p = 0.003	F = 2.36 R ² = 0.03 p = 0.066
Sub-daily FO	F = 18.35 R ² = 0.16 p = 0.003	F = 31.25 R ² = 0.31 p = 0.003	F = 41.47 R ² = 0.33 p = 0.003	F = 5.38 R ² = 0.03 p = 0.003	F = 12.46 R ² = 0.10 p = 0.003	F = 13.23 R ² = 0.07 p = 0.003

Table A9. P-values of associated species scores extracted from non-metric multidimensional scaling of occurrence/relative abundance and frequency of occurrence. Sub-daily FO is measured by the proportion of one-hour intervals in a day that species were sighted on each day at the sites. Significant species scores are shown in bold ($p < 0.05$).

Species	Occurrence and relative abundance	Sub-daily FO
Whitetip reef shark	0.012	0.001
Pelagic thresher	0.001	0.001
Grey reef shark	0.014	0.001
Tiger shark	0.001	0.001
Silvertip shark	0.023	0.001
Scalloped hammerhead	0.100	0.001
Oceanic manta	0.002	0.312
Hawksbill sea turtle	0.001	0.060
Spotted eagle ray	0.882	0.318
Whale shark	0.076	0.876
Torpedo ray	0.837	0.570
Cowtail sting ray	0.599	0.609

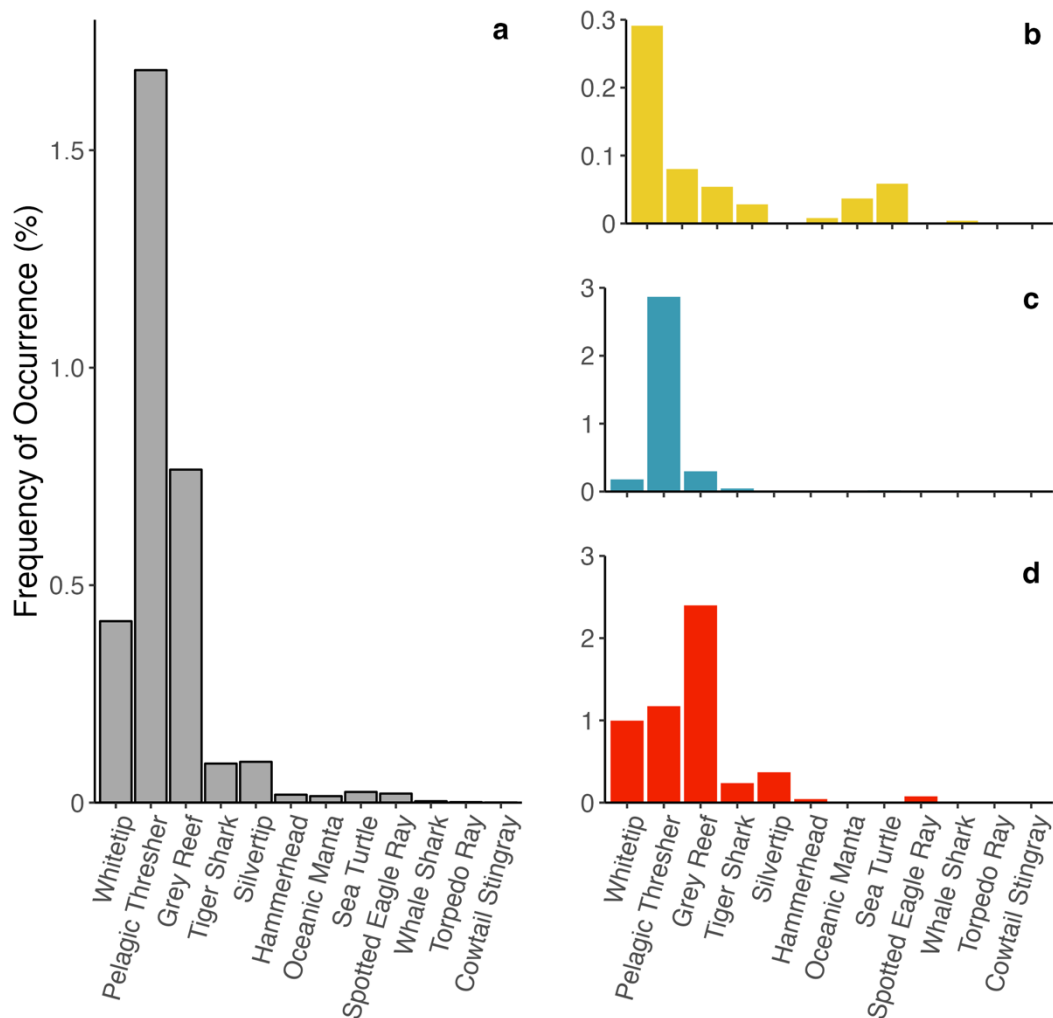


Figure A1. Frequency of occurrence measured by the proportion of **images** that species were observed overall (a) and at Hudhekede (b), Kedevari (c), and Farikede (d). All values represent a percentage.

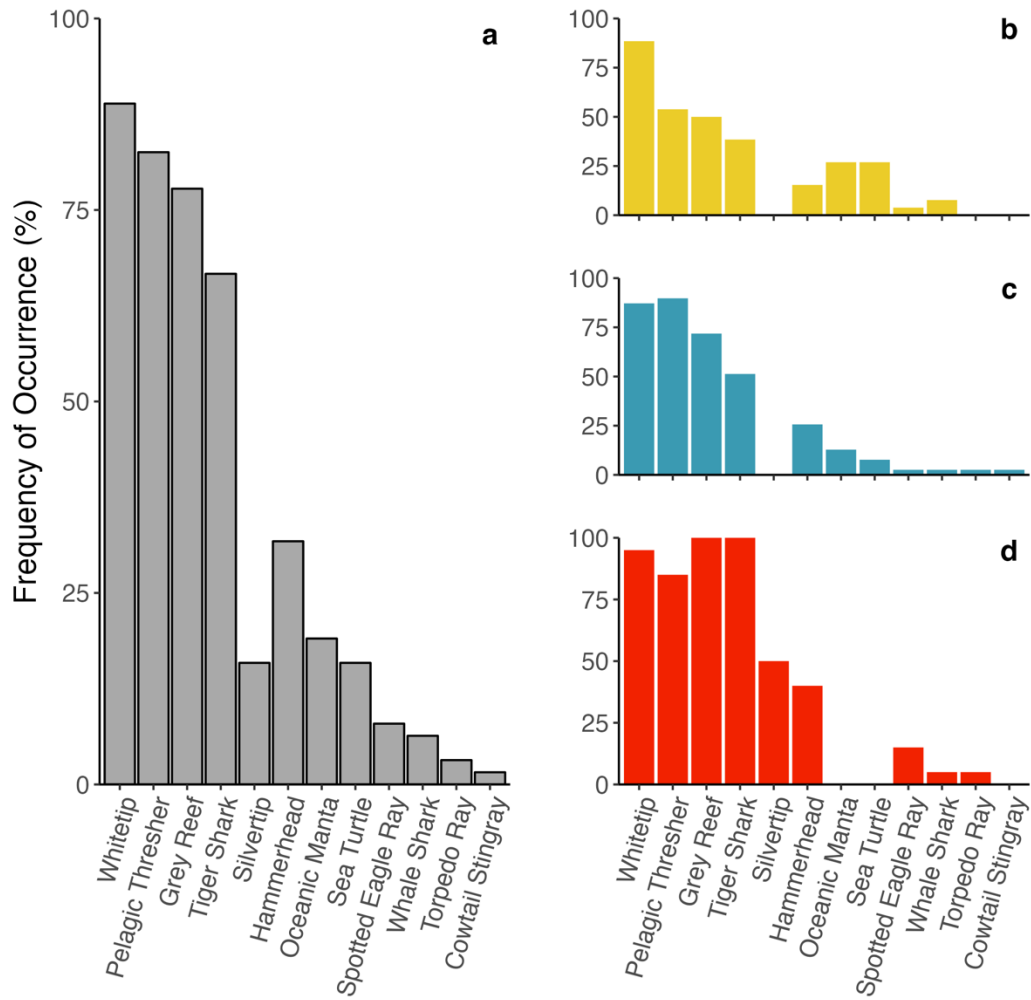


Figure A2. Frequency of occurrence measured by the proportion of **days** that species were observed overall (a) and at Hudhekede (b), Kedevari (c), and Farikede (d). All values represent a percentage.

Appendix B: Supplemental information for Chapter 3

Contingent Valuation Survey

Intro:

We are conducting this anonymous survey to better understand how tourists feel about contributing to conservation initiatives in Fuvahmulah Atoll. The project is conducted in collaboration with local council, dive operators and the Maldives Environmental Protection Agency and will inform management plans to protect Fuvahmulah's biodiversity.

This survey is being conducted purely for research purposes in accordance with the Market Research Society Code of Conduct and won't be used to sell or market anything to you on an individual basis. The survey will take about 15 minutes to complete.

By submitting your survey responses, you will have the opportunity to enter your email for a chance to win 1 year membership to [The Cyclone](#), or a Manta Ray [Adoption Package](#).

Please note that your name and email will remain confidential and will not be linked with any of your survey answers.

The contact information collected for the prize will be stored separately from your survey responses and destroyed once the incentive has been administered.

By clicking '>', you acknowledge that you have read and agree to the [privacy policy](#).

By clicking the next button below, it is assumed that you have read the accompanying letter of information, understood the above details of the experiment, and freely consent to participate.

Q1 Which of the following best describes you?

This is a single response item

Maldivian national visitor

International visitor

Local resident of Fuvahmulah

If local resident is selected;

Since this study is assessing the perceptions of tourists, we are only collecting responses from visitors at this time.

Please feel free to share this survey with national and international visitors in Fuvahmulah.

Thank you for your time.

Q2 Which, if any, of the following interactions have you had with sharks and/ or rays previously?

This is a multi-response item

- Participated in research
- Encountered while scuba diving, snorkelling, and/or freediving
- Participated in diving, snorkelling and/or freediving trips focusing on encounters with sharks or rays
- Watched movies or documentaries focused on sharks and/or rays
- Visited an aquarium which displays sharks and/or rays
- Other (please specify)
- I have never encountered sharks and/ or rays in any of these ways

Q3 Have you heard that sharks and rays have been experiencing global population declines?

This is a single response item

- Yes
- No
- Unsure

Q4 Have you heard that shark and ray populations are vulnerable to population declines because they reproduce slowly?

This is a single response item

- Yes
- No
- Unsure

Q5 How do you feel about the decline of sharks and rays over the recent decades?

This is a table item. Users select one heading for each option

Please choose one

<i>Options</i>	<i>Headings</i>
1	Not at all concerned
2	Slightly concerned
3	Moderately concerned
4	Very concerned
5	Extremely concerned

preQ6 We would now like to show you a short video clip. If you are on a limited bandwidth connection, please indicate this below:

This is a single response item

- Continue to video
- I'm on a limited bandwidth connection

volCheck Please ensure your volume is turned up for the next question...

This item requires no user response

introQ6a Please take a moment to watch this video. The following questions will be based on the information provided in the video.

This item requires no user response

(script read in video and text displayed on pdf version for limited bandwidth)

Because of its unique diversity on land and the reefs, Fuvahmulah Atoll was declared a UNESCO Biosphere Reserve in 2020.

Community stakeholders and Fuvahmulah City Council are considering additional conservation actions to safeguard and protect the biodiversity of Fuvahmulah; however, long-term funding plans for these actions need to be addressed.

Since tourism can provide economic opportunities for local communities, we would like to know your opinion on different conservation initiatives that would work toward protecting Fuvahmulah's nature.

Proposed conservation actions include;

Community Education

Because of the exposed nature of Fuvahmulah Atoll, it has been historically difficult for many young children to learn how to swim and proper swim safety.

For this reason there are limited opportunities for marine science students to gain practical experience and training beyond the classroom.

Funds for community education initiatives would support swimming lessons for local school students, field trips for marine science students to more accessible regions, and paid internships with Fuvahmulah Nature Park, or Fuvahmulah Biosphere Reserve.

Waste Management

Plastic pollution is a primary environmental concern for Fuvahmulah.

Funds for waste management will contribute to a water plant where reusable bottles may be filled and will fund reverse osmosis water filtration systems that can be installed to local houses and businesses.

Local business and households may also be supplied with reusable bags to eliminate the need for plastic bags.

Management of Protected Areas

Management plans for current protected areas need to be developed, and additional protected areas may be designated through monitoring efforts.

Park rangers must be hired to ensure that all sites are effectively protected and well-managed.

Funds for protected area management will support staff and other operational cost of monitoring the reserve's protected areas.

Marine Research and Education Centre

To support visiting and local researchers, a marine research and education centre would provide laboratory space, storage and essential equipment. Additionally, the centre would serve as an educational space for local students and tourists where they can visit to learn about the maritime history of the island, local marine ecosystems and current research efforts.

Funds for the Marine Research and Education Centre would contribute to local staff salaries, including a director, research officer, and education manager.

While the following questions seem hypothetical, please remember that your answers will be considered by Fuvahmulah City Council and will impact policy design.

The amount you state may be accepted as the charge for visiting this area in the future.

This item requires no user response

(included only at the end of low bandwidth pdf version) Please note: Time has been allowed for you to read the information fully, the 'next' button will appear shortly.

checkQ6 Were you able to see and hear the video?

This is a single response item

Yes

No, I'm on a limited bandwidth connection

No, I had a problem with the video

Q6 Considering your income and current expenses, slide the bar to indicate how much (USD) you would be willing to pay as a Fuvahmulah Atoll entry fee if those funds were to be divided among the projects outlined in the video?

This fee would be a one-off charge collected by your guest house once for your trip rather than a daily fee or a fee per dive.

If you need to check the latest foreign currency exchange rates you can find one here.

This question has format RangeSlider

Q7 How certain are you of your previous answer?

This is a single response item

Uncertain

Somewhat uncertain

Somewhat certain

Certain

Q8 Who do you feel should be primarily responsible for paying this fee?

This is a single response item

Visitors accessing marine protected areas only

Visitors accessing land-based protected areas only

Visitors accessing either marine or land-based protected areas

All visitors to Fuvahmulah Atoll

Don't know

Other (please specify)

Q9 At what price (USD) would an entrance fee be so low that you'd be worried it wouldn't make a difference in protecting Fuvahmulah's biodiversity?

This fee would be a one-off charge collected by your guest house once for your trip rather than a daily fee or a fee per dive. Assume the fee would be spilt equally between the previous mentioned initiatives.

If you need to check the latest foreign currency exchange rates you can find one here.

This is a single response item

- \$10 or less
- \$25
- \$50
- \$75
- \$100
- \$125
- \$150
- \$175
- \$200
- \$250
- \$300 or more

Q10 At what price (USD) would an entrance fee become so expensive that you would be less likely to visit Fuvahmulah in the future?

This fee would be a one-off charge collected by your guest house once for your trip rather than a daily fee or a fee per dive. Assume the fee would be spilt equally between the previous mentioned initiatives.

If you need to check the latest foreign currency exchange rates you can find one here.

This is a single response item

- \$10 or less
- \$25
- \$50
- \$75
- \$100
- \$125
- \$150
- \$175
- \$200
- \$250
- \$300 or more

Q11 How you would like your contributions to be distributed amongst the different conservation initiatives proposed?

Please select a value from 0% to 100% for each initiative. Your entries need to total to 100%.

This is a numeric table item. Users enter a number (from 0-100) for each option under each heading.

Headings

Community Education

Waste Management

Marine Protected Areas Management

Marine Research Centre

Q12 Please select the answer that best explains your thoughts on the Fuvahmulah entrance fee.

This is a multi-response item

I feel I cannot afford to pay more to contribute to these conservation initiatives

I'm not interested in contributing to these conservation initiatives

I don't believe the money gained by fees will be spent responsibly on conservation initiatives

I feel the money for these initiatives should come from other places and not from tourists

I can't decide without more time or information

I didn't understand the question

Other (please specify)

Q13 To ensure all questions are being read properly, please select manta ray from the list below:

This is a single response item

Whale shark

Mola mola

Manta ray

Devil ray

Hammerhead shark

Q14 Have you been a member of an environmental NGO or non-profit within the last 5 years?
(by member we include both paid and/or volunteer work)

This is a single response item

Yes

No

Q15 Have you previously contributed financially to a non-profit organization?

This is a single response item

Yes

No

Q16 Was it a conservation charity focusing on ecosystem or wildlife protection?

This is a single response item

Yes

No

Q17 Which activity listed below is your primary activity in Fuvahmulah?

This is a single response item

Please select the option which applies best to you

Snorkelling

Freediving

Scuba Diving

Other (please specify)

Q18a How frequently do you travel specifically to snorkel?

This is a single response item

- More than once per year
- Approximately once per year
- Once every 1-3 years
- Less than once every 3 years

Q18b How frequently do you travel specifically to free dive?

This is a single response item

- More than once per year
- Approximately once per year
- Once every 1-3 years
- Less than once every 3 years

Q18c How frequently do you travel specifically to scuba dive?

This is a single response item

- More than once per year
- Approximately once per year
- Once every 1-3 years
- Less than once every 3 years

Q19a Prior to this trip, how many times have you visited Fuvahmulah to snorkel?

This is a single response item

- Once
- Twice
- Three to five times
- More than five times
- I have never visited Fuvahmulah to snorkel before

Q19b Prior to this trip, how many times have you visited Fuvahmulah to free dive?

This is a single response item

- Once
- Twice
- Three to five times
- More than five times
- I have never visited Fuvahmulah to free dive before

Q19c Prior to this trip, how many times have you visited Fuvahmulah to scuba dive?

This is a single response item

- Once
- Twice
- Three to five times
- More than five times
- I have never visited Fuvahmulah to scuba dive before

Q20 You mentioned your primary activity in Fuvahmulah is \$Q17.
How would you describe your skill level in this activity?

This is a single response item

- Beginner
- Intermediate
- Advanced
- Professional

Q21 Which type of excursion do you most prefer?

This is a single response item

Blue water excursions
at these sites, divers / snorkelers / freedivers drift off the reef and into the blue water with the aim of encountering large sharks, oceanic manta rays or other species that are found off the reef (example in Fuvahmulah is Farikedde, also known as Plateau).

Reef excursions
at these sites, divers / snorkelers / freedivers follow the reef encountering corals, reef sharks, turtles and occasionally other species such as tiger sharks or thresher sharks

No preference

Q22 Did you come to Fuvahmulah to encounter specific marine organisms?

This is a single response item

- Yes
- No

Q23 Which marine organisms motivated your visit?

This is a ranked item. Users can rank items in sequence

Please select your top 3 choices, with 1 being the top choice

- Hammerhead sharks
- Thresher sharks
- Manta rays (oceanic or reef)
- Tiger sharks
- Whale sharks
- Cetaceans (dolphins and whales)
- Corals
- Other marine organisms

Q23.1 (if other was selected) Which other marine organisms motivated your visit?

This is a free text item

Q24 Which of the following marine animals have you encountered in Fuvahmulah on this trip so far?

This is a multi-response item

- Hammerhead sharks
- Thresher sharks
- Manta rays (oceanic or reef)
- Tiger sharks
- Whale sharks
- Cetaceans (dolphins and whales)
- I have not been in / on the water in Fuvahmulah
- I have been in / on the water in Fuvahmulah, but have not encountered any of the above animals

flashQ25 The following section is a set of questions that are part of a standardized international survey. We're interested to know how you feel about various issues relating to the environment and conservation.
This item requires no user response

Q25 (NEP scale) Looking at the following statements, please indicate how much you agree or disagree with each statement:

This is a table item. Users can select one heading for each question

Question

1. We are approaching the limit of the number of people the earth can support
2. Humans have the right to modify their environment to suit their needs
3. When humans interfere with nature it often has disastrous consequences
4. Human ingenuity will ensure that we do NOT make the earth unliveable
5. Humans are severely abusing the environment
6. The earth has plenty of natural resources if we just learn how to develop them
7. Plants and animals have as much right as humans to exist

8. The balance of nature is strong enough to cope with the impacts of modern industrial nations
9. Despite our special abilities humans are still subject to the laws of nature
10. The so-called "ecological crisis" facing humankind has generally been greatly exaggerated
11. The earth is like a spaceship with very limited room and resources
12. Humans were meant to rule over the rest of nature
13. The balance of nature is very delicate and easily upset
14. Humans will eventually learn enough about how nature works to be able to control it
15. If things continue on their present course we will soon experience a major ecological catastrophe

Heading

Strongly Disagree
 Disagree
 Neither agree nor disagree
 Agree
 Strongly agree

C1 Which of the following options most closely aligns with your gender?

This is a single response item

- Male
- Female
- I prefer to identify in another way
- Prefer not to say

C2 Please indicate your age:

This is a single response item

- Under 21
- 21-24
- 25-34
- 35-44
- 45-54
- 55-64
- 65+
- Prefer not to say

C3 Please indicate your annual household income:

If you need to check the latest foreign currency exchange rates you can find one here.

This is a single response item

- Under \$20,000
- \$20,000-\$39,999
- \$40,000-\$59,999
- \$60,000-\$79,999
- \$80,000-\$99,999
- \$100,000-\$149,999
- \$150,000-\$199,999
- \$200,000-\$499,999
- \$500,000 or more
- I'd rather not say

C4 What is the highest level of education you have achieved?

This is a single response item

- Elementary / middle school graduate (grades 8-10)
- High school graduate (grades 9-12)
- Some post-secondary education
- Bachelor's degree / associate's degree
- Doctorate / master's degree / professional degree
- I'd rather not say
- Other (please specify)

(Incentive)

Thank you for taking part in our survey! If you would like the chance to win a Manta Trust prize pack (either an annual membership to The Cyclone or a Manta Adoption Pack) please enter your details below.

Your details will be stored separately from survey answers in order to ensure the survey remains anonymous. Your details will not be linked to your survey answers.

Please see our Privacy Policy for more information on how we look after your personal information. You can change your mind about us contacting you or storing your personal data at any time by emailing us at info@mantatrust.org.

Data Protection & Providing Consent:

Your privacy is important to us, so we will always keep your details secure and never use them for marketing communications that you haven't agreed to receive. We will never share your information with a third party.

By supplying your contact details below, you consent to the Manta Trust storing the personal data you're submitting in this form. You also confirm that you've read and agree with our Privacy Policy, and you're happy for the Manta Trust to use this personal data to contact you about the prize draw.

This item requests a list of text responses

First Name:

Last Name:

Email Address:

To provide any additional feedback or comments, please use the space provided below.

This is a free text item

End

We have now reached the end of the survey. Thank you for participating. You may now close your window.

This item requires no user response

Table B1. Committed vs. casual classification method of snorkelers, freedivers, and scuba divers visiting Fuvahmulah Atoll.

		Frequency of dive tourism related trip			
		Travel > 1/per year	Travel 1/per year	Travel 1/every 1-3 years	Travel <1/every 3 years
Skill level	Beginner	Committed	Casual	Casual	Casual
	Intermediate	Committed	Committed	Casual	Casual
	Advanced	Committed	Committed	Casual	Casual
	Professional	Committed	Committed	Committed	Casual

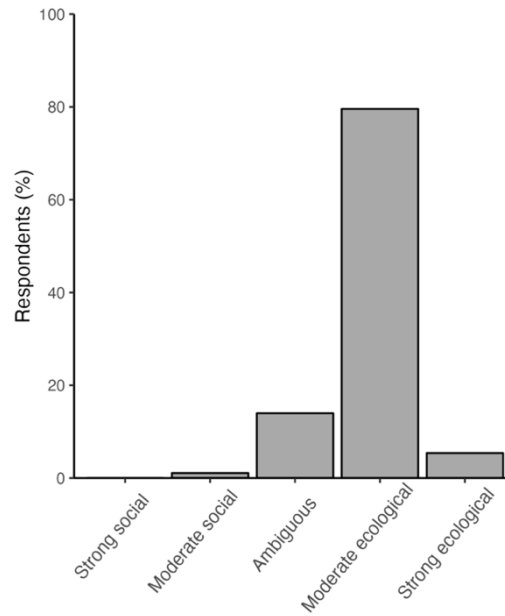


Figure B1. Percentage of respondents ($n = 93$) within each New Ecological Paradigm scale category: strong dominant social paradigm, moderate dominant social paradigm, ambiguous worldview, moderate ecological worldview, and strong ecological worldview.

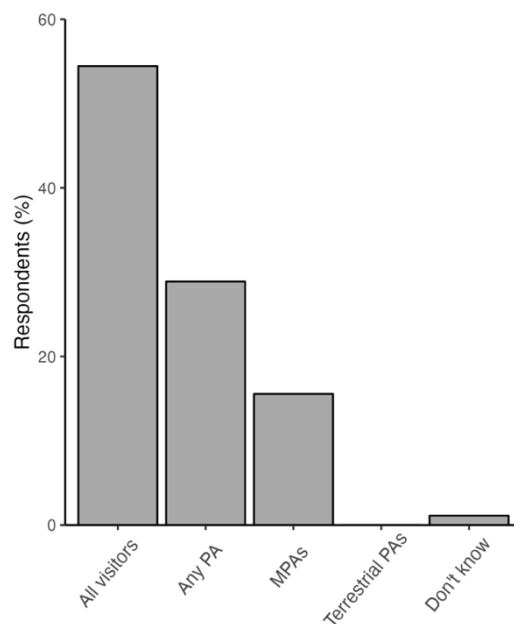


Figure B2. Percentage of respondents (n = 90) who feel the one-time “Reserve” entrance fee should be paid by all visitors, visitors accessing protected areas (PA) only, marine protected areas only, terrestrial protected areas only, and those who answered, “I don’t know”. Only respondents who answered with positive WTP were presented this question.

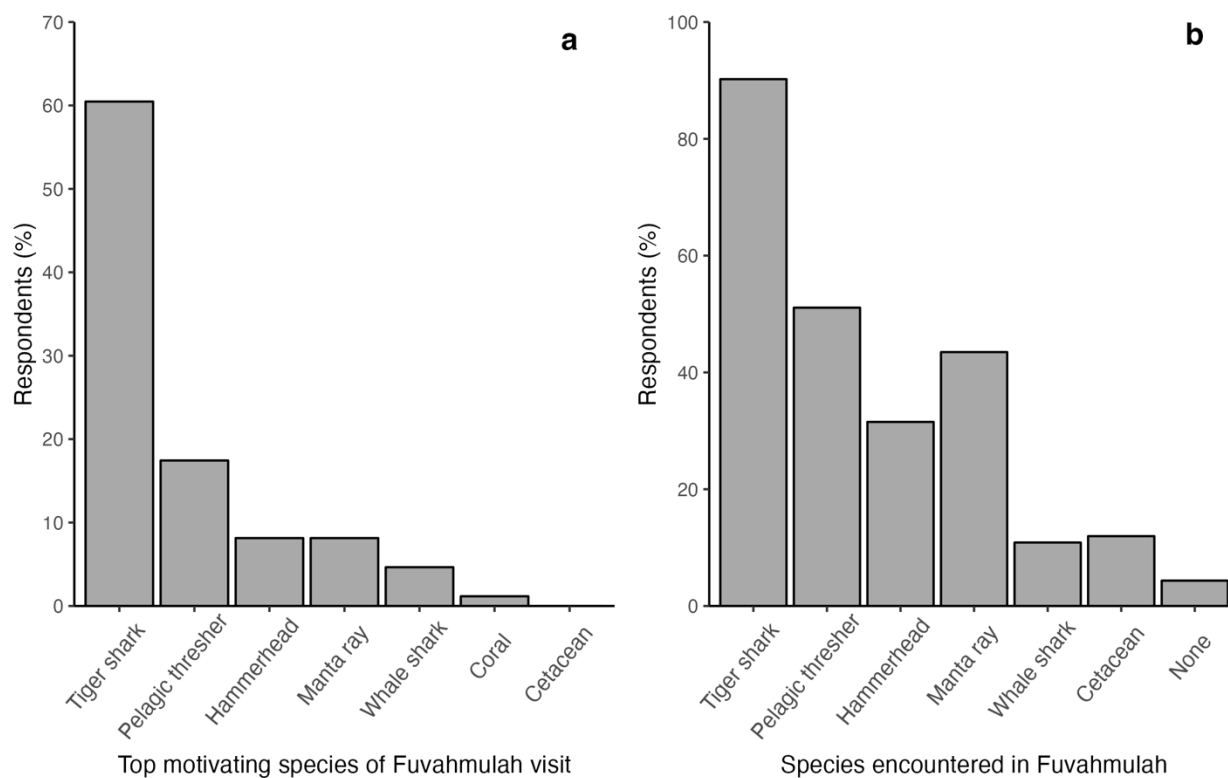


Figure B3. The top motivating species (a) for respondents' trip to Fuvahmulah of those who indicate their trip was motivated by a specific encounter ($n = 86$) and the reported encounters for dive tourists ($n = 92$) during their visit in Fuvahmulah (b).