



## Eyes on the Reef

Using remote cameras at cleaning stations to understand the seasonality and behaviour of the reef manta rays (*Mobula alfredi*) of Laamu Atoll, Maldives.

Author: Christopher John Stewart Wenham

Supervisors: Phil Doherty & Jasmine Corbett

I certify that this dissertation is entirely my own work and no part of it has been submitted for a degree or other qualification in this or another institution and give permission for a copy to be held by my supervisor and distributed at their discretion.



## Abstract

Reef manta rays (*Mobula alfredi*) are highly conspicuous, with a large subpopulation located in the Maldives. *M.alfredi* significantly contribute towards the country's economy through tourism; providing incentive to enhance protections of the species and their aggregation sites. To enforce sustainable tourism activities, behaviours and environmental drivers of spatial-temporal occurrence must be understood to provide scientific guidance to ensure effective conservation management.

A singular cleaning station in Hithadhoo Corner, Laamu Atoll was investigated using remote-camera systems to monitor *M.alfredi* between June 2021 - 2022. Generalised Linear Models were used to investigate the relationship between influencing factors and *M.alfredi* abundance. Temperature was the most significant environmental predictor, presence decreased as temperatures neared threshold values (30°C). Moon phase proved to be a non-significant predictor, higher visitation rates during the First Quarter were assumed to result from the lack of productive foraging opportunities and enhanced need for cleaning after feeding events. Tidal phase showed no significant effect, higher abundances were seen during low tide, this is attributed to optimal feeding conditions in nearby areas at high tide. Highest abundance was seen at the beginning or turn of monsoons, suggesting these months provided favourable cleaning and courtship conditions. Human presence did not affect abundance, despite consistent dives operating within the area. Sex and maturity of 57 identified individuals differed, 40 individuals revisited, indicating strong site-fidelity to this area. Occurring in groups of up to 3 individuals, social behaviour may be an important driver of aggregations, independent of environmental factors.

These findings both compliment and oppose existing studies, indicating environmental and anthropogenic variables vary per geographic location. It is recommended that monitoring of

Hithadhoo Corner is continued to provide further robust data analyses. Enforcement within the area is a priority alongside the implementation and distribution of the manta interaction code of conduct.

## Table of Contents

<i>Abstract</i> .....	2
<i>Introduction</i> .....	8
Monitoring large mobile marine vertebrates.....	8
<i>Mobula alfredi</i> – The Reef Manta Ray.....	9
Threats to <i>M.alfredi</i> .....	10
Economic benefits & Tourism.....	11
Marine Protected Areas and Management .....	12
Environmental Influence & Importance of Cleaning Stations .....	13
Aims .....	14
<i>Methodology</i> .....	15
Study area location.....	15
Survey design .....	16
Data collection.....	17
Data cleaning.....	19
Data analysis .....	22
<i>Results</i> .....	23
Assessing the indices available to represent <i>M.alfredi</i> abundance and presence .....	23
Influence of environmental factors.....	23
Moon Phase .....	23
Tide Phase .....	25
Temperature.....	25
Influence of human presence.....	27
Behavioural Patterns – Visitation, Site fidelity & Interaction .....	28
Visitation .....	28
Site affiliation .....	30
Sex and Maturity Status.....	31
<i>Discussion</i> .....	32
Influence of environmental factors.....	32
Moon Phase .....	32
Tidal Phase .....	33
Temperature.....	35
Influence of human presence.....	36
Behavioural Patterns – Visitation, Site affiliation & Status.....	37
Visitation .....	37
Site affiliation .....	39
Sex & Maturity Status .....	40
Recommendations for Hithadhoo Channel Protected Area.....	41
Limitations & Future Study .....	43
<i>Conclusion</i> .....	44

<i>Acknowledgements</i> .....	45
<i>References</i> .....	46
<i>Supplementary Information</i> .....	67
<b>Supplementary Figures</b> .....	67
<b>Supplementary Tables</b> .....	75

## List of Tables

**Table 1: Results from each Pearson’s correlation coefficient test (r and p values) for all possible combinations of the four indices available to represent *M.alfredi* abundance..... 16**

## List of Figures

**Figure 1: Map of Laamu Atoll with the location of the protected area expansion that includes Hithadhoo Corner marked blue and Hithadhoo Channel Protected Area highlighted in blue; nearby island Olhuveli the location of Six Senses Laamu resort. All other inhabited islands are labelled. Laamu Atoll in relation to the rest of Maldives Archipelago is shown highlighted in grey on the inset map on the right..... 17**

**Figure 2: Photographs of the EOTR system: (A,B) The secure placement of the two different systems on ‘shallow block’ in an upwards facing direction; (C,D) The primary EOTR system within a custom-made camera housing; (E,F) The secondary EOTR system including the internal structure; (G) The HOBO water temperature logger attached to the reef..... 19**

**Figure 3: Photographs of manta ray’s individual ventral spot patterns. (A) the primary (yellow) and secondary (red) areas of identification (Stevens, 2016); (B) Photograph of MV-MA-3754 ‘Baby Maya’ taken by EOTR at Hithadhoo Corner on 26/02/2022. Variations in ventral pattern markings (C) and dorsal shading (D) Reproduced from Stevens, 2016..... 22**

**Figure 4: The presence (presence score) of *M.alfredi* over the year between June 2021 – June 2022, with each moon phase highlighted..... 25**

**Figure 5: The number of individuals present at hours from low (light blue) and high tide (dark blue)..... 26**

**Figure 6: The temperature and presence score at Shallow Block, Hithadhoo Corner, for each day recorded over the survey year..... 27**

**Figure 7 - The probability of M.alfredi occurrence at Shallow Block, Hithadhoo Corner over different temperatures. Shaded area detail standard error..... 28**

**Figure 8 - Human presence and highest MaxN of each surveyed month..... 29**

**Figure 9 – The largest MaxN value and mean encounter time of each month. Annotated number of days recorded within the month on top of each bar..... 30**

## Introduction

### Monitoring large mobile marine vertebrates

Accommodating the conservation needs for large mobile marine species, such as elasmobranchs, is a major challenge in marine management (Scales et al., 2014). These species fulfil critical ecosystem roles, but there remains a lack of adequate protection throughout their ranges (Heithaus, 2008). Despite growing protective measures, these species remain vulnerable to various environmental and anthropogenic pressures, which can result in dramatic declines (Scales et al., 2014; Stevens, 2016). Effective conservation is problematic, many mobile marine vertebrates, encompass large ranges throughout their lifetime, producing the problem of conserving a moving target (Scales et al., 2014). Therefore, it is crucial that critical habitat which facilitates mating, feeding, cleaning, and migration are identified and protected; continued access to these areas is essential to minimise disturbances to fitness and survival (Heithaus et al., 2008; Stevens, 2016). In addition, understanding how populations use their environment and the identification of factors that influence this allows the quantification of threats which aids in effective mitigation (Powles et al., 2000; Harris et al., 2020). Long-term observational studies provide insight to selective pressures, behavioural activity, and social structures within a population. Due to the long-lived nature of large mobile species, datasets are essential to develop reliable and accurate information for conservation decisions (Jacoby et al., 2012; Stevens, 2016; Perryman et al., 2019).

Much understanding of marine ecosystems has been founded on data collected from Underwater Visual Censuses (UVC); which have been developed to assess communities, individuals, and ecosystems to reduce knowledge gaps and aid environmental management decisions (Dickens et al., 2011). Previously multi-year studies in the marine realm were constrained both financially and logistically (Strayer et al., 1986). The advent of affordable



technology has increased the potential for easily repeatable long-term studies; over the past 45 years remote camera systems have become a popular tool due to their effectiveness in assessing marine assemblages; reducing limitations and bias of UVC methodologies (Harvey et al., 2007; Mallet and Pelletier, 2004). With the future intensification of climate change, the identification environmental drivers, and habitat dependency patterns, will indicate areas and seasons where priority protection is needed to enable effective conservation management throughout the species range (Stewart et al., 2018; Peel et al., 2019; Harris et al., 2020).

### *Mobula alfredi* – The Reef Manta Ray

Reef manta rays (*Mobula alfredi*) are highly conspicuous, large planktivorous elasmobranchs, belonging to the *Mobulidae* family, which includes ten species (Harris et al., 2020; White et al., 2017). Distributed circumglobally, occurring from 36°S to 40°N, *M.alfredi* are found throughout tropical and sub-tropical waters of the Indo-Pacific Ocean (Supplementary Figure S1) (Stevens, 2016). Populations are highly fragmented as their movement is intrinsically linked to resource and habitat requirements, which is dependent on frequenting continental coastal reefs, remote oceanic islands, and archipelagos, often venturing offshore to the mesopelagic zone (Kashiwagi et al., 2011; Kitchen-Wheeler et al., 2012; Braun et al., 2014; McCauley et al., 2014; Stevens, 2016; Stewart et al., 2018; Armstrong et al., 2020; Harris et al., 2020; Harris and Stevens, 2021). Long-term sighting records suggest the species is highly philopatric, only undertaking short migrations to form aggregations at favoured sites (Strike et al., 2022). This aggregation behaviour involves sub-populations conducting the majority of their activities at hotspot locations which consist of discrete habitat, such as cleaning stations, to engage in social and reproductive activities (Harris et al., 2021).

## Threats to *M.alfredi*

In recent decades, *M.alfredi* population declines have been a result of targeted and bycatch fisheries, driven by the international demand of mobulid gill plates for use in the Asian medicine market (O'Malley et al., 2016; Lawson et al., 2016). A report from 2011, shows manta species contributed towards 44% of the \$11.3million mobulid market (O'Malley et al., 2013). As a result, both manta species were listed on Appendix II of the Convention on International Trade in Endangered Species (CITES) and the Convention on Migratory Species of Wild Animals (CMS), ensuring trade would not threaten survival throughout *M.alfredi*'s range (Lawson et al., 2016). However, population declines are accelerated by conservative life history traits which include slow growth, late maturity, and low fecundity; the potential recovery after population depletion is reduced (O'Malley et al., 2013; Dulvy, et al., 2014a; Dulvy et al., 2014b; Stevens, 2016; Stewart et al., 2018). The small size of subpopulations, migratory and aggregating behaviour make *M.alfredi* particularly vulnerable to over-exploitation and habitat destruction (Dulvy et al., 2014b). Substantial population declines have occurred on a global scale, threatening *M.alfredi* survival; a cause of local and potential broadscale extinctions (Peel et al., 2019). As a result, *M.alfredi* is currently listed as 'Vulnerable' on the IUCN Red List of Threatened Species (Marshall et al., 2018). The targeting of individuals from critical habitats is a particular concern, however, protections set by the Maldivian Environmental Protection Agency in 2014 dictate it is illegal to capture, keep, or harm any type of ray, as determined in the Batoidea Maldives Protection Gazette No. (IUL) 438-ECAS/438/2014/81 (Couturier et al., 2012; Kitchen-Wheeler et al., 2012; EPA, 2014; Harris and Stevens, 2021). In addition to anthropogenic affects such as entanglement in marine debris and boat strikes, habitat degradation, and coastal development, irresponsible tourism activities continue to impact the species at key ecologically important aggregation sites (Deakos et al., 2011; O'Malley et al., 2013; Harris et al., 2020; Murray et al., 2020). These

pressures are amplified by climate change; sea-level rise has the potential to impact the availability of zooplankton, the primary food source of *M.alfredi* (Richardson, 2008).

### Economic benefits & Tourism

Despite the economic value of *M.alfredi* to local economies, tourism is likely to be negatively impacting manta rays (Stevens, 2016). However, it provides an attractive economic alternative to the consumptive use of this species, which aids in driving protective legislation nationally and internationally (O'Malley et al., 2013; Lawson et al., 2016; Stevens, 2016). The non-consumptive value is not only ecologically beneficial but economically sound; within ecotourism, a single manta can be worth \$1million alive rather than \$500 dead over its lifetime (Cisneros-Montemayor & Sumalia, 2010; O'Malley et al., 2013; Hani et al., 2019). It is estimated manta tourism will contribute ~US\$140 million annually to the global economy (O'Malley et al., 2013; Murray et al., 2019). Well-managed models are proven to generate sustainable livelihoods, whilst providing a long-term solution to conserving marine megafauna (Supplementary Figure S1) (O'Malley et al., 2013; Hani et al., 2019). At local levels, where few other sources of income exist from fishing, communities will significantly benefit financially from ecotourism (Garrod, 2004). However, tourism has grown substantially in the Maldives over the last decade, with over 1.7 million visitors in 2019, the Maldives face increased pressure on natural resources (Ministry of Tourism, 2019; Murray et al., 2019). Anderson et al., 2011b found that tourists within the Maldives were willing to pay more for excursions involving manta rays than sharks and turtles. However, close human contact can have a significant effect on manta behaviours, resulting in feeding cessation (Murray et al., 2019). Within the Maldives only 44% of human-manta interactions complied with existing guidelines (Murray et al., 2019). Codes of conduct produced by organisations such as The Manta Trust, provide a guideline to minimise disturbance from tourists (Murray et al., 2019).

## Marine Protected Areas and Management

The Republic of the Maldives supports the largest known sub-population of *M.alfredi* globally and was estimated to generate US\$8.1 million annually (2006-2008) from ecotourism activities; but without proper measures, ecotourism could be detrimental to survival (Anderson et al., 2010b; Stevens, 2016; Strike et al., 2022). The Manta Trust aims to provide scientific guidance to aid governments and non-governmental organisations (NGOs) to make informed and effective marine management decisions (Manta Trust, 2021). Since the charities' inception over 5000 *M.alfredi* have been identified, making the Maldivian population the largest and most intensively studied population globally (Manta Trust, 2022). Since 2005 the Maldivian Manta Ray Project has played a direct role in gaining national protection for manta rays, but on-going monitoring of habitats such as cleaning stations is crucial to assess the effectiveness of these protective measures. The Manta Trust has successfully driven the designation of two marine protected areas (MPAs) in the Maldives, assisting in the development and implementation of management plans that enforce strict regulations and sustainable tourism activities within these areas of key manta habitat (Manta Trust, 2022).

Despite all ray species being protected from target fisheries in the Republic of the Maldives, a small total combined area is protected by the existing 42 Marine Protected Areas (MPAs) equates to 116.3km<sup>2</sup>, 0.5% (21,596 km<sup>2</sup>) (EPA, 2014; Stevens and Froman, 2019). Currently only one MPA, Hanifaru Bay, Baa Atoll has a management plan with in-situ enforcement of regulations; all other MPAs are, in theory, paper parks (Stevens and Froman, 2019). By targeting key aggregation sites of *M.alfredi* populations, MPA management can direct resources and efforts towards areas where populations will experience the best benefits of protection, additionally the development of strong legislation can help evolve paper parks into well-protected and enforced areas (Kessel et al., 2017; Lawson et al., 2017). However, the

success of MPA design and implementation relies on the understanding of seasonality and behaviour of target species at different sites (Peel et al., 2019).

### Environmental Influence & Importance of Cleaning Stations

*M.alfredi* follow productive ocean hotspots across the archipelago, with the biannual change in winds and ocean currents to exploit rich zooplankton feeding grounds (Kitchen-Wheeler et al., 2012; Stevens, 2016). The migratory behaviour of the Maldivian subpopulation is strongly influenced by the South-Asian Monsoon (Anderson et al., 2011a; Gischler et al., 2014). This drives currents that enhance productivity on the leeward side of the atolls through deep-water upwellings that bring nutrient-rich water to the surface (euphotic zone); additionally influencing increases in abundance of zooplankton (Samsal, 2006; Diek et al., 2017; Armstrong et al., 2021). The southwest monsoon (*Hulhangu*) occurs from May to October whilst the northeast (*Iruvai*) occurs from December to March. November and April are considered transitional periods, though this can be highly variable changing to October and March (Anderson et al., 2011a; Aslam and Kench, 2017). These biannual seasonal migrations determine aggregation site use and predominant exhibited behaviour activities (Nicholson-Jack et al., 2021). During the monsoon, shallow reefs with nearby productive channels and lagoons are favoured by *M.alfredi* due to the concentration of prey (Stevens, 2016).

Cleaning stations consist of either prominent reef outcrops or coral bommie structures, primarily where megafauna including *M.alfredi* are cleaned by symbiotic cleaner wrasse which remove ecto-parasites and detritus left from feeding (Rohner et al., 2013; Stevens, 2016). In addition, cleaning stations may experience aggregations of *M.alfredi* for other reasons: metabolic state and physiological functions, such as gestation and digestion which are enhanced in the warmer shallow waters of cleaning stations (Hight and Lowe, 2007; Jirik and

Lowe, 2012; Thums et al., 2013; Stevens, 2016; Nickelson-Jack et al., 2021). Secondly, courtship and mating behaviour has primarily been reported in these areas; facilitating a focal point to gather and socialise (O’Shea et al., 2010; Rohner et al., 2013; Stevens, 2016; Harris and Stevens, 2021). Furthermore, stations can act as a refuge from predators such as pelagic sharks (Marshall and Bennet, 2010). Due to the potential of observing important social behaviours, the study of aggregation sites and environmental drivers can contribute to filling critical knowledge gaps within manta ray conservation (Krüger, 2020). Multiple environmental drivers are noted to influence movement patterns of elasmobranchs (Rohner et al., 2013; Schlaff et al., 2014; Harris et al., 2020). This study shall focus on the following factors: moon phase, tidal phase, water temperature, encounter time, time of day and time of season (month). These factors have previously been shown to affect planktivorous elasmobranchs occurrence at cleaning stations (O’Shea et al., 2010; Rohner et al., 2013; Barr and Abelson, 2019).

## Aims

The ‘Eyes on the Reef’ study will build upon existing knowledge of the *M. alfredi* population of Laamu Atoll through long-term monitoring over a year using remote camera systems, offering an insight into manta ray abundance without the bias of human presence (Harvey et al., 2007). This research is necessary to provide robust, scientific guidance to local and national governance, communities, and ecotourism operators to maintain successful sustainable manta tourism activities and use of the site. The study aims to provide results to aid in management plans by: (1) understanding the temporal variation of cleaning station habitat use and the environmental drivers of this; (2) assessing the impacts of ecotourism to site use by *M. alfredi* and (3) investigating behavioural patterns at the cleaning station without the presence of humans.

## Methodology

### Study area location

The Republic of the Maldives is 870km long from 7° North to 0.5° South of the equator in the Indian Ocean (Harris et al., 2020). Hithadhoo Corner (1°47'53.76"N 73°24'35.99"E), in the southwest of Laamu Atoll (Haddhunmathi Atoll), features a significant manta aggregation site featuring five separate cleaning stations ranging in depths of 15-22m, known collectively as 'manta point': Shallow Block, Split Block, Yellow Block, Turtle Block, and The Ridge. A single cleaning station, 'Shallow Block' was sampled from June 2021 – June 2022. The site, which is used regularly by local and liveaboard dive operations, provides consistent manta encounters due to its proximity to atoll channels, manta's favoured feeding areas (Stevens, 2016). Currently discussions are ongoing on whether Hithadhoo Corner will be included within the nationally designated Hithadhoo Channel Protected Area (HCPA) (Blue Marine Foundation, *pers comms*). Five other new sites within Laamu are protected due to their biologically important reef ecosystem, location of various globally endangered species, spawning aggregation sites, channels, mangroves and has been declared a 'Hope Spot' by non-profit Mission Blue (Figure 1) (Ministry of Environment, Climate Change and Technology, 2021; Mission Blue, 2021). Currents within the area vary regularly with the change in tide, swell towards the nearby surf break 'Ying Yang' can intensify current strength; mixing of water influences upwellings that provide high production levels of nutrients (Anderson et al., 2011). Cleaner fish species including Blunthead Wrasse (*Thalassoma amblycephalum*), Lyretail Wrasse (*Thalassoma lunare*) and Blue-streak Cleaner Wrasse (*Labroides dimidiatus*) are most prevalent within the area and are regularly observed (Stevens et al., 2018a).

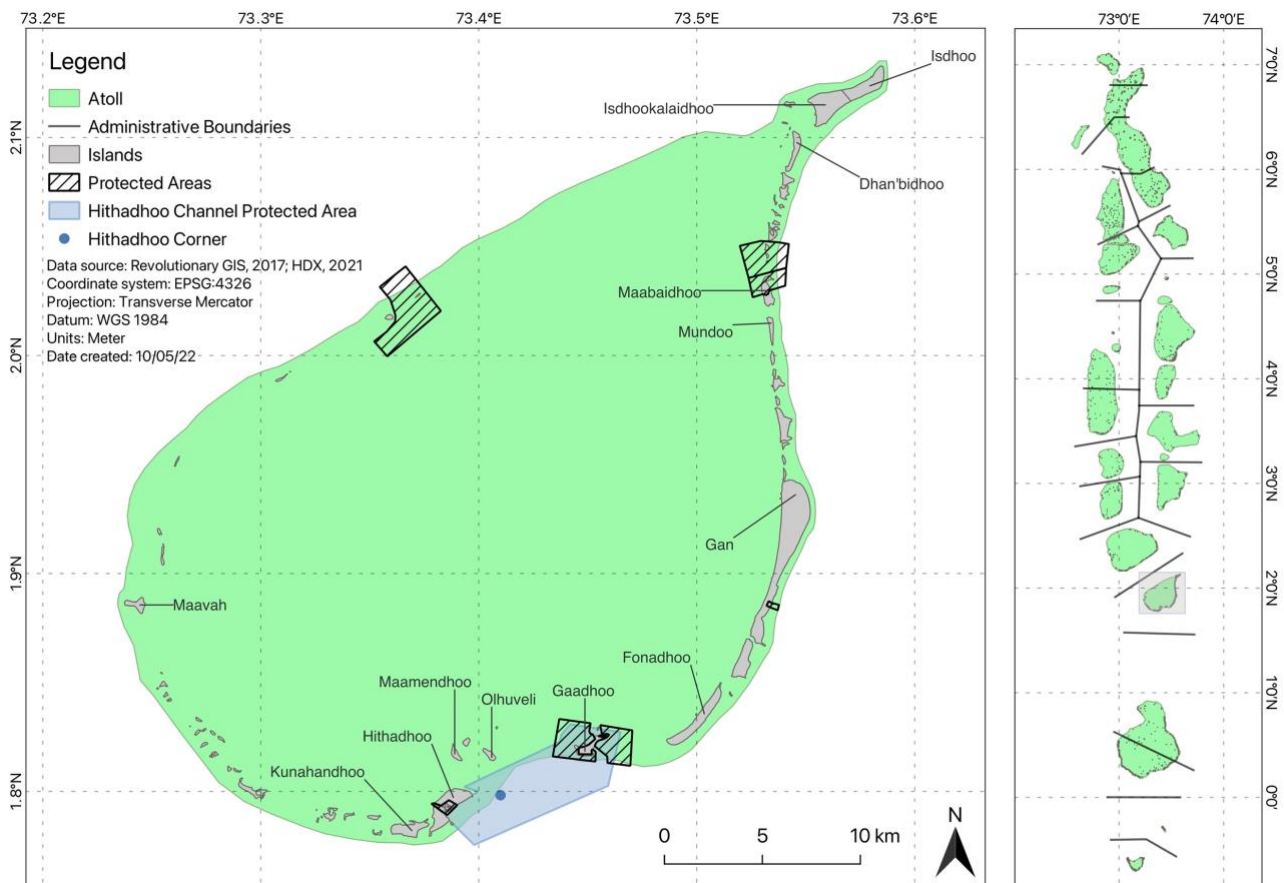


Figure 1 - Map of Laamu Atoll with the location of the protected area expansion that includes Hithadhoo Corner marked blue and Hithadhoo Channel Protected Area highlighted in blue; nearby island Olhuveli the location of Six Senses Laamu resort. All other inhabited islands are labelled. Laamu Atoll in relation to the rest of Maldives Archipelago is shown highlighted in grey on the inset map on the right.

## Survey design

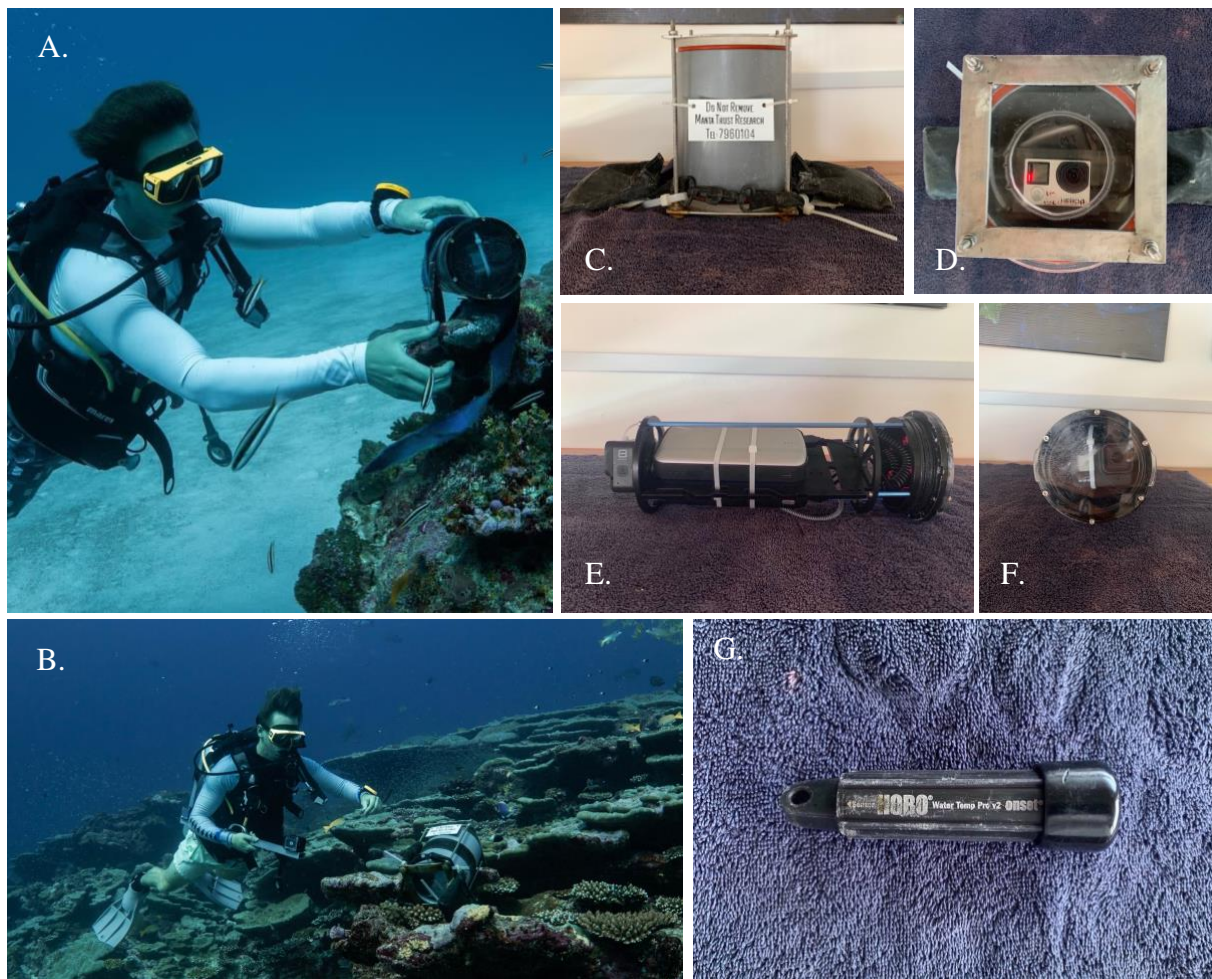
The cleaning station was chosen based on a period of short-term trials by the Eyes on the Reef (EOTR) system on the various cleaning stations of Hithadhoo Corner between March and May 2021. The Manta Trust concluded that a higher number of *M. alfredi* individuals were observed on Shallow Block, which also included higher densities of cleaner wrasse and higher coral cover; with particularly healthy acropora (MUI, 2021 *unpublished*). Remote Underwater Photography (RUP) provides long term observation of manta behaviour without the biases of human presence, which additionally solves the data collection limitations associated with SCUBA based observations including time and depth (Mallet and Pelletier, 2014). Literature shows that remote camera systems successfully record more mobile species than other visual



survey techniques and allows for improved standardisation over long time periods (Stobart et al., 2007; Colton and Swearer, 2010).

### Data collection

To collect data the EOTR system included a GoPro Hero 4 Camera (San Mateo, USA; resolution 1080p; fps 30; mode wide angle) connected to a Voltaic battery pack (V75; 19,200mAh; Brooklyn, USA) within a custom-made housing (Figure 2c-d; dimensions 23.5 x 16.5 x 16.5 cm). Another EOTR system was used whilst the primary system was retrieved to collect data and recharge, this featured a Go Pro Hero 8 with the same settings connected to two Voltaic battery packs (Figure 2e-f; dimensions 33.5 x 12 x 12 cm). The RUP system was consistently placed on the same area of reef which provided a field of view of a large area of the cleaning station. The front end was secured using a weight-belt strap whilst the back end of each housing featured two weight bags (4kg), to ensure the camera was directed in an upwards facing position (Figure 2a-b).



*Figure 2 - Photographs of the EOTR system: (A,B) The secure placement of the two different systems on 'shallow block' in an upwards facing direction; (C,D) The primary EOTR system within a custom-made camera housing; (E,F) The secondary EOTR system including the internal structure; (G) The HOBO water temperature logger attached to the reef.*

The RUP system was programmed to record from sunrise and finish after sunset. Through online scheduling systems including GoPro Labs (San Mateo, USA) and BlinkCam (Vancouver, Canada) recordings were set to last periods of up to 12 hours, though this time could vary; recordings stayed within the timeframe of 05:59 to 20:00. Using the GoPro's timelapse setting, photos were taken every minute during this time frame for each recording. This control of image acquisition allowed for improved standardisation of data over long time periods (Stobart et al., 2007). Overall, 166,772 photos were taken during a total period of 267 days between June 2021 and June 2022.

Each day the moon phase, average water temperature (°C) and high tide time were recorded. Moon phase was recorded through online moon phase calendars (<https://www.timeanddate.com/moon/phases/maldives/male>), the beginning of each phase was noted within the data. Average water temperature was recorded hourly using a HOBO Water Temperature Pro V2 logger ( $\pm 0.2^{\circ}\text{C}$ ; Bourne, USA), in which the logger was located next to the attachment point for the EOTR systems. Tidal charts were provided by the Maldives Meteorological Service (<https://meteorology.gov.mv/>). The highest high tide time was recorded if both high tides occurred during the day's survey time; if there was a singular high time during the survey time, it would be recorded even if it was not the day's highest; the same method was used for low tide. If a tide phase did not fall within survey time, the closest time would be chosen. The mid-point between high and low tide was used to define the state of the ebb and flood tide.

### Data cleaning

Firstly, the number of *M.alfredi* within each photo was counted per survey day; start and end survey time were additionally noted. 'Sighting events' were created for each day, which included, sighting event time (beginning and end), duration and maximum number of *M.alfredi* seen in one photograph (MaxN). It was likely that a *M.alfredi* present at the cleaning station would not be recorded in every photo as photos were taken every minute, and the camera's field of view can limit how much of the manta ray is captured. Because of this a 'sighting event' would continue despite the lack of manta ray presence. If a manta ray was not seen within >10 minutes of the previous sighting, the 'sighting event' would be terminated, it was assumed the individual would have departed from the cleaning station, the following encounter would be considered a new 'sighting event'. If MaxN reached >2, the sighting event was

identified as a peak manta encounter. Primary behaviour observed of the manta rays within each survey day was defined as ‘cleaning’ if the sum of encounters lasted longer than 2 minutes and ‘cruising’ if not. Diver and snorkeller presence at the cleaning station recorded by the EOTR was recorded in a similar fashion to sighting events.

Secondly, available photos of individual manta’s ventral spot patterns were set aside for identification. Ventral spots are unique to each individual, much like a fingerprint, making individuals identifiable (Kitchen-Wheeler, 2010). Using the markings between gills slits, lower abdomen, and pectoral fins, patterns could be variable (Figure 3). All photo identifications were manually matched to individuals of the ‘Laamu Atoll – Branchial Identification Gallery’ which features 138 individuals known to be present within Laamu Atoll; if not found the ‘Maldivian Master Branchial Gallery’ featuring ~5000 manta rays was consulted (Supplementary Figure S2). Individuals are assigned a new identification code if found to be unidentified.

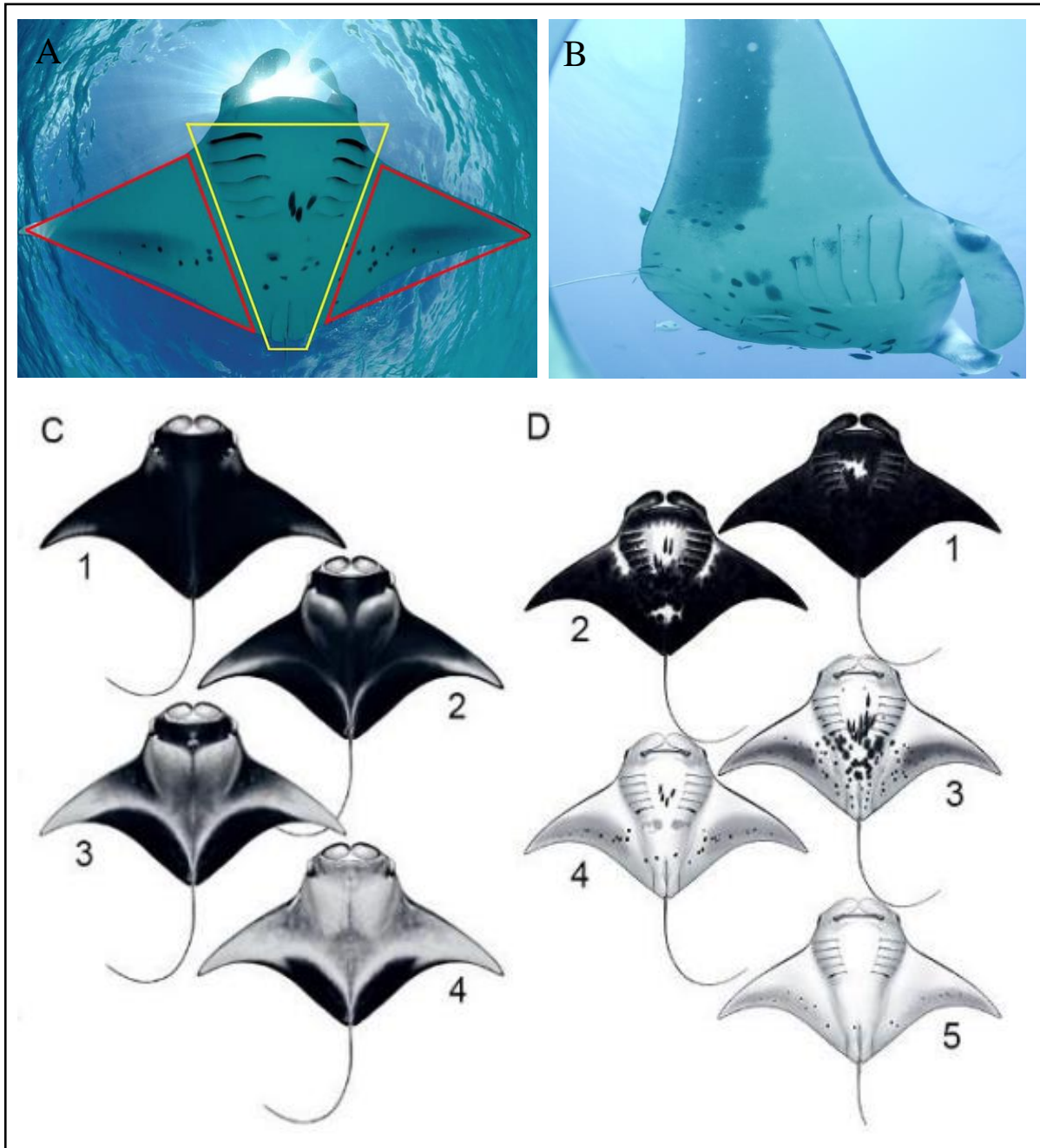


Figure 3 - Photographs of manta ray's individual ventral spot patterns. (A) the primary (yellow) and secondary (red) areas of identification (Stevens, 2016); (B) Photograph of MV-MA-3754 'Baby Maya' taken by EOTR at Hithadhoo Corner on 26/02/2022. Variations in ventral pattern markings (C) and dorsal shading (D) Reproduced from Stevens, 2016.

## Data analysis

All statistical testing was undertaken using RStudio (Version 1.4.1106; R Core Team, 2013) at a significance level of  $\alpha = 0.05$ . A Pearson's correlation co-efficient was calculated to test the linear relationship between different indices used to represent *M.alfredi* abundance and presence, as well as relationships between different environmental variables through the 'stats' package (R Core Team, 2013). A Generalised Linear Model (GLM) was used to identify any significant effect of environmental variables (Moon Phase - Full, First Quarter, New, Third Quarter; Temperature - °C; Mean encounter time (minutes) and Tide – Time until high tide (hours)) upon MaxN via the 'stats' package (Supplementary Table S1,S2) (R Core Team, 2013). One additional model was built to investigate effects human presence (n) on MaxN (Supplementary Table S3). MaxN was used throughout abundance analyses, it is considered a suitable conservative measurement of estimated abundance for remote camera systems (Campbell et al., 2015; Stobart et al., 2015; Campbell et al., 2018; Sherman et al., 2018; Whitmarsh et al., 2018). Poisson distribution and 'log' link function were used within these models, as there was no overdispersion. Using backwards stepwise selection, the model was reduced to determine significant environmental variables; versions of the GLM model were compared to others using an ANOVA with an analysis of deviance ( $t = \text{'Chisq'}$ ) to acquire p values. An additional binomial GLM was used to identify the effect of the same environmental variables on the probability of occurrence; the model was fitted with binomial family and 'logit' link function, this model also underwent the same backwards stepwise selection and analysis of deviance as the others (Supplementary Table S4,S5). If a variable showed significant difference a Tukey post-hoc test was used to determine variability within categorical variables. Two separate One-way ANOVAs were run to investigate the effect of human presence on mean encounter time (Supplementary Table S6) and the effect of the number of days recorded on MaxN (Supplementary Table S7). Model assumptions and residuals of one-

way ANOVAs, linear models and GLMs were checked using diagnostic plots and the ‘DHARMA’ package (Hartig, 2016). Descriptive statistics were used to further describe the data.

## Results

### Assessing the indices available to represent *M.alfredi* abundance and presence

There are four different indices that represent *M.alfredi* abundance and presence; MaxN, Estimated Number of Manta Rays, Presence Score (number of photos featuring manta rays per day/total number of photos per day) and Presence (yes or no presence). Primary statistical analysis was performed using MaxN, and secondary analysis using Presence. However, for graphical depiction other indices were chosen due to their suitability to present the different circumstances within the data. Results from Pearson’s correlation coefficient tests show that all indices are positively correlated with each other, as a result they are all used to represent *M.alfredi* abundance and presence throughout this report (Table 1).

Table 1 – Results from each Pearson’s correlation coefficient test (*r* and *p* values) for all possible combinations of the four indices available to represent *M.alfredi* abundance.

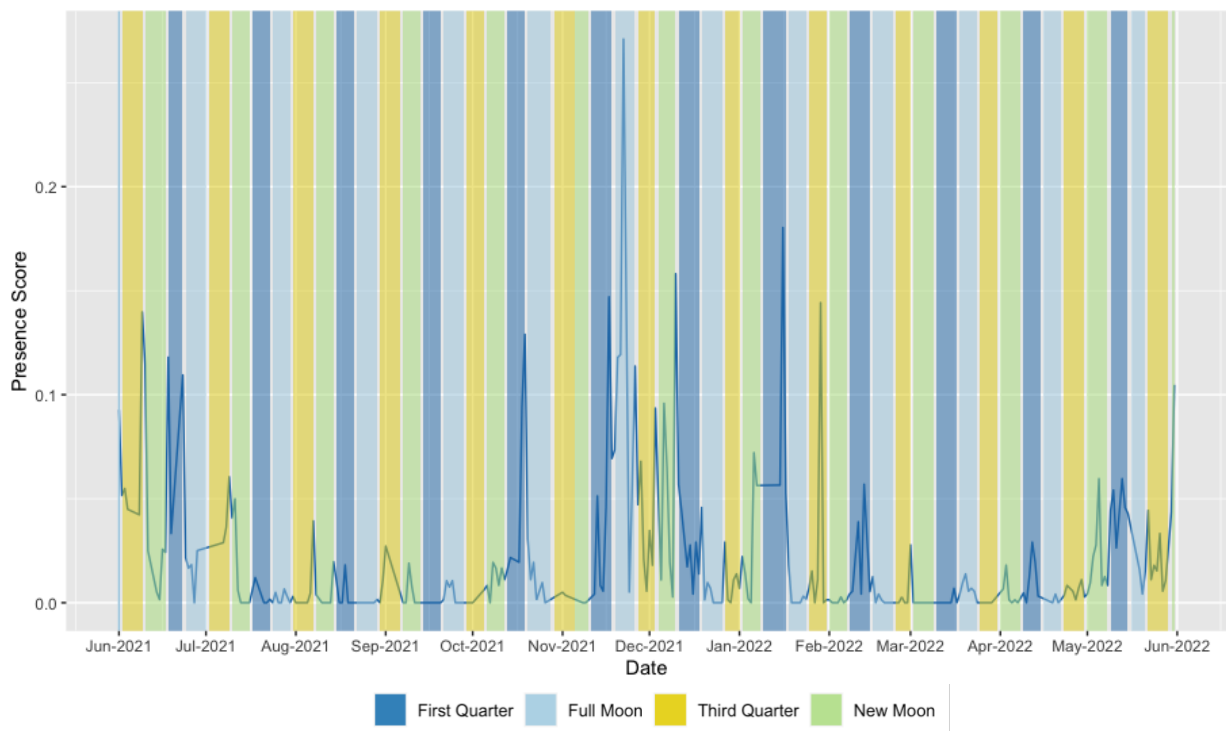
		<b>MaxN</b>	<b>Estimated Number</b>	<b>Presence Score</b>	<b>Presence</b>
<b>MaxN</b>	<i>r</i>		0.720314	0.6206019	0.7473727
	<i>p</i>		<0.0001	<0.0001	<0.0001
<b>Estimated Number</b>	<i>r</i>			0.6875066	0.5132287
	<i>p</i>			<0.0001	<0.0001
<b>Presence Score</b>	<i>r</i>				0.3687703
	<i>p</i>				<0.0001

### Influence of environmental factors

#### Moon Phase

Moon phase did not have a significant impact on *M.alfredi* abundance (MaxN) ( $\chi^2_{3} = 27.536$ ,  $p = 0.75101$ ). There were peaks in presence throughout the year, especially during First Quarter and Full Moon phases, smaller peaks in abundance occurred during Third Quarter phase

(Figure 5). Peaks in abundance primarily occurred between mid-October and February; 22<sup>nd</sup> November was scored the highest abundance (0.27) (Figure 4). A secondary peak was experienced over June 2021 over multiple moon phases. This is replicated in June 2022, where a rise in abundance occurs (Figure 4). First Quarter had the largest mean MaxN of 1.22, whilst the mean MaxN of Full Moon, Third Quarter, and New Moon were similar (Supplementary Figure S3).



*Figure 4 - The presence (presence score) of M.alfredi sightings over the year between June 2021 – June 2022, with each moon phase highlighted.*

Using sighting data between June 2021 and June 2022 the probability of *M.alfredi* occurrence at Hithadhoo Corner over different Moon phases was calculated. There was no effect of Moon Phase of probability of occurrence ( $\chi^2_1 = 12.059$ ,  $p = 0.6239$ ), probability ranged from 74.5% during First Quarter to 70.2% during the New Moon (Supplementary Figure S4).



## Tide Phase

Tide state did not have a significant effect on MaxN ( $\chi^2_1 = 26.532$ ,  $p = 0.65101$ ). However high ( $r_{265} = 0.1794165$ ,  $p = 0.003263$ ) and low ( $r_{265} = 0.1578946$ ,  $p = 0.009762$ ) tide times are significantly correlated with Moon Phase, however, both had small correlation co-efficient. Peaks in manta sightings were seen 1 hour before high tide and 3 hours after low tide (Figure 5). In addition, the binomial model revealed tide state did not have a significant effect on the probability of occurrence ( $\chi^2_1 = 11.821$ ,  $p = 0.9607$ ) (Supplementary Figure S5).

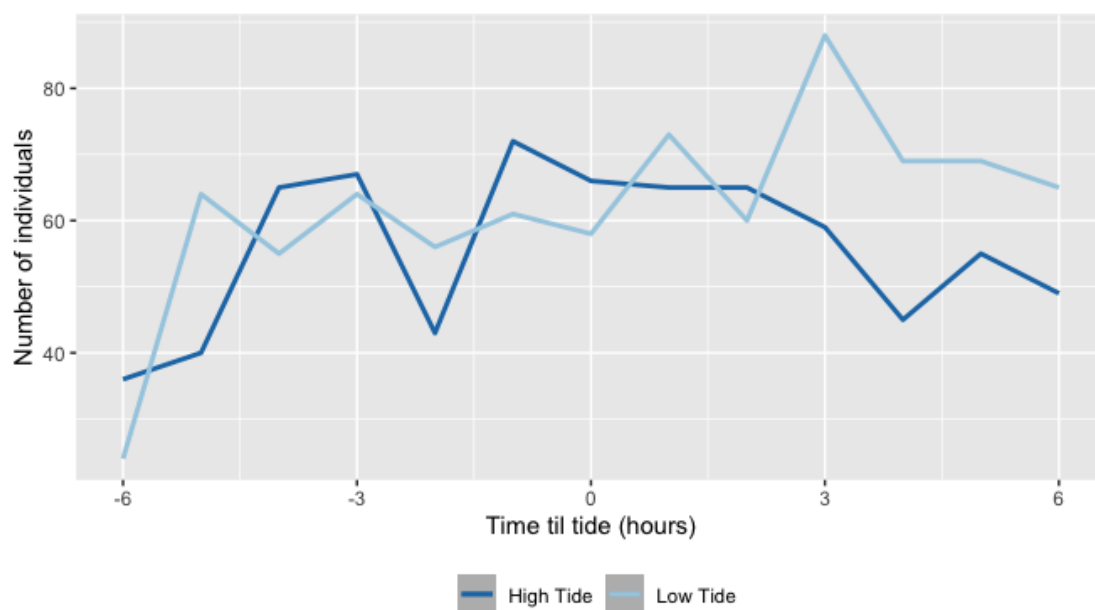


Figure 5 – The number of individuals present at hours from low (light blue) and high tide (dark blue).

## Temperature

Over the year temperatures stayed with the range of 26.15°C – 29.96°C. A decreasing trend in temperatures occurred from mid-September to mid-November. Abnormalities in temperature were seen either side of January 2022; a substantial drop to 27.07°C and rise to 29.95°C from temperatures around 28°C range. A clear increasing trend from mid-March to the beginning of April was seen, temperatures then plateaued before decreasing again in May which experienced both the lowest (26.15°C) and highest (29.96°C) temperatures (Supplementary Figure S6).

Temperature data from June 2021 to 13<sup>th</sup> June was not acquirable, hence is missing from the dataset. A large proportion of presence scores >0.1 occurred in between the 28 – 29°C range. With favourable temperatures either side of 28.5°C with the highest presence scores. Presence score slowly diminishes after temperatures reach 29.2°C (Figure 6).

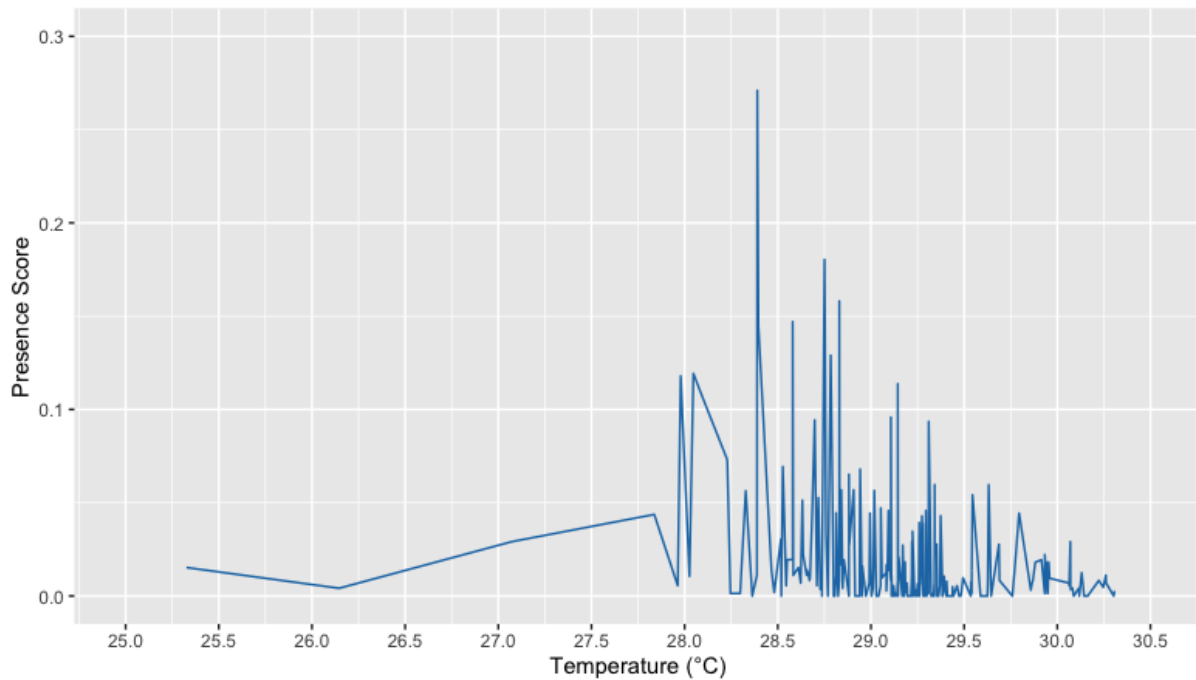


Figure 6 - The temperature and presence score at Shallow Block, Hithadhoo Corner, for each day recorded over the survey year.

Results from a best fit GLM model revealed that temperature had significant influence on *M.alfredi* abundance ( $\chi^2_1= 165.22$ ,  $p = 0.0404$ ). However, due to missing high-resolution data values at the beginning of the study, we are unable to draw this as an absolute conclusion. The probability of occurrence of *M.alfredi* decreases significantly if temperatures are greater than 28°C. It is >90% likely for individuals to occur in temperatures ~26°C and is < 60% likely for individuals to occur in temperatures ~30°C (Figure 7). Additionally, the binomial model revealed that temperature had a significant effect on probability of occurrence ( $\chi^2_1= 295.61$ ,  $p = 0.02829$ ).

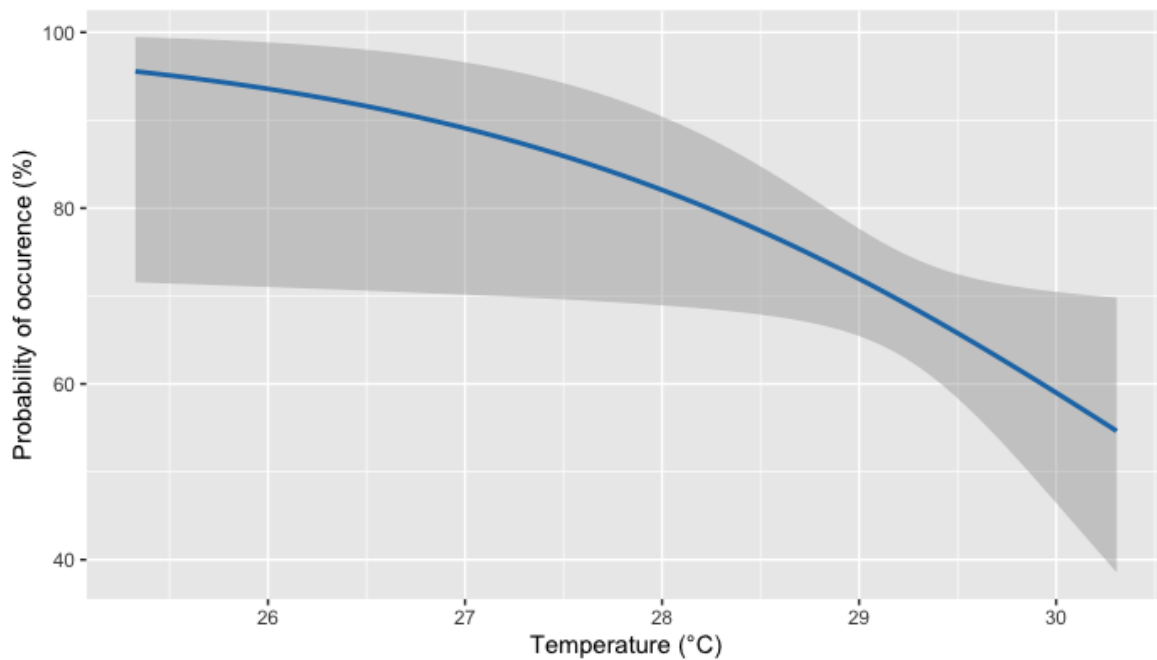


Figure 7 - The probability of *M.alfredi* occurrence at Shallow Block, Hithadhoo Corner over different temperatures. Shaded area detail standard error.

### Influence of human presence

To assess the influence of human presence on *M.alfredi* abundance, MaxN of each month was plotted against monthly number of humans. Surprisingly, months with higher human presence display larger MaxN values, as seen in November, December, January, April and May. Mean encounter time is mostly seen to be lower in the presence of humans apart from the months of January, May, and December. March (n = 13) and April (n = 20) have the highest human concentrations and some of the lowest encounter times (6.06 minutes, 4.65 minutes) (Supplementary Figure S7). July to September features the lowest human concentrations coupled with encounter time of lower ranges (Figure 8). Results from a GLM found that human presence does not have a significant effect on MaxN ( $\chi^2_1 = 210.09$ ,  $p = 0.7719$ ) or monthly mean encounter time (One-way ANOVA;  $F_{1,10} = 0.0422$ ,  $p = 0.8413$ ) (Supplementary Table S6).

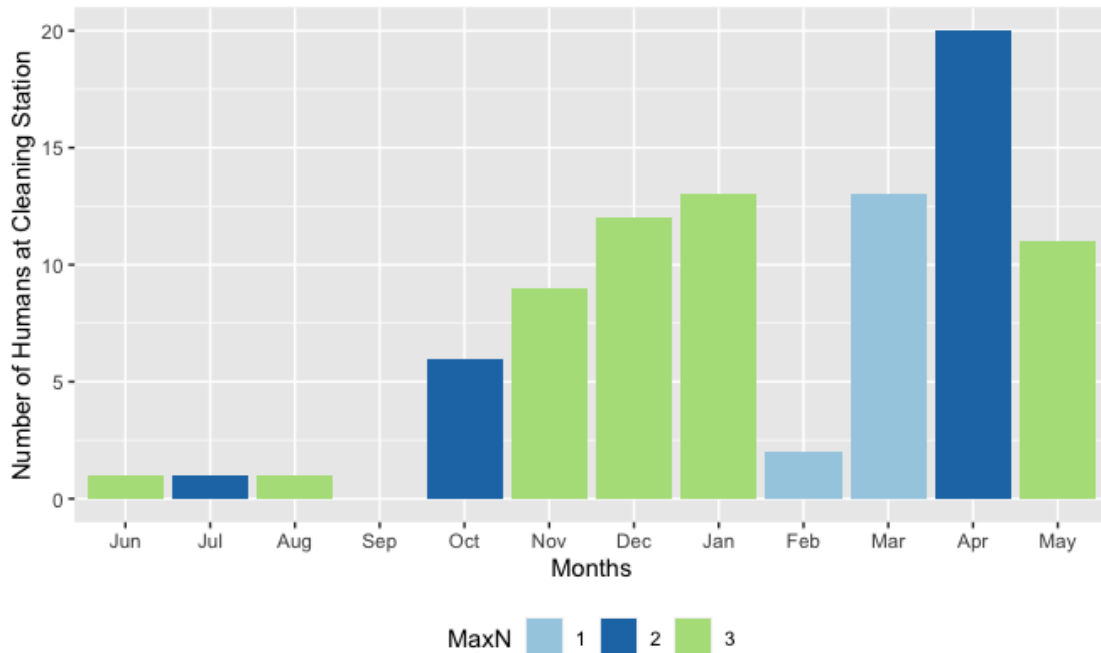


Figure 8 - Human presence and highest MaxN of each surveyed month.

## Behavioural Patterns – Visitation, Site fidelity & Interaction

### Visitation

With a total of 886 sighting events, almost a half (49.44%) lasted for  $\leq 1$  minute; it is assumed these were cruising past the cleaning station and not stopping to clean. Cleaning behaviour lasted between 2 and 177 minutes (mean = 13.74 minutes), with around 47.40% of individuals staying between 2 and 40 minutes; 2.14% staying for periods longer than 1 hour (Supplementary Figure S8). Sighting events of  $\leq 1$  minute were excluded when assessing the number of manta rays that clean together. 76.12% of all manta rays were observed to clean alone, the remaining 23.88% were observed to clean in groups of two or three. There were only 10 occurrences where three manta rays were seen together (Supplementary Figure S9).

To understand why encounter time varied, mean encounter time was investigated with MaxN. Encounter time had a significant effect on MaxN ( $\chi^2_1 = 186.75$ ,  $p < 0.001$ ). In most cases, the months with longer mean encounter time experienced larger MaxN values. 5 out of the 6

months with a MaxN of 3 had longer encounter times, compared to months with MaxN values of 1 and 2. This trend continued, most months with MaxN of 2 experienced prolonged encounter times compared to February and March; MaxN 1. Manta rays would stay at the cleaning station longer in the presence of other individuals (Figure 9). The mean time spent at the cleaning station peaked in November (66.95 mins) and was lowest in August (3.81 min). Both peaks (October – November & May – June) lie within the south-west monsoon season. Throughout each month, some days were not recorded, a one-way ANOVA was used to investigate the bias of months with more recorded days, revealing that the number of days recorded doesn't have significant effect on resultant MaxN ( $F_{1,10}=2.5288$ ,  $p=0.1429$ ) (Supplementary Table S7).

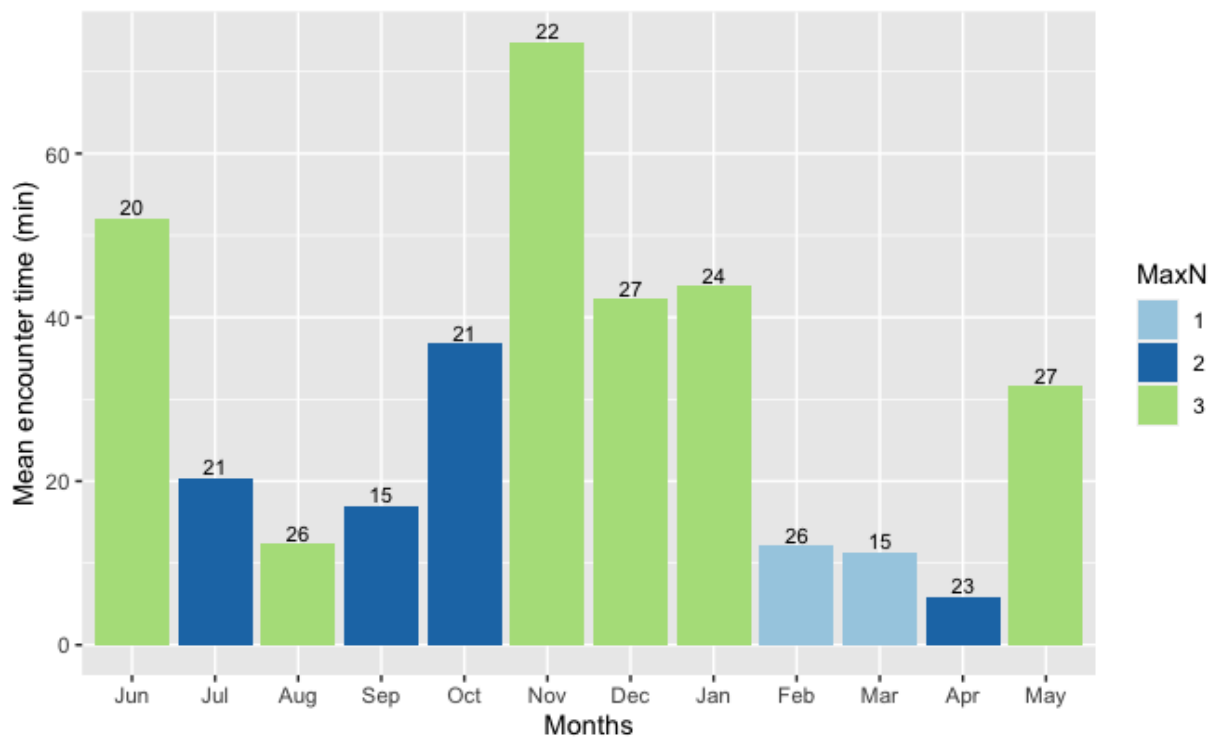


Figure 9 – The largest MaxN value and mean encounter time of each month. Annotated number of days recorded within the month on top of each bar.

Peak sighting events contain  $\geq 2$  individuals. November (39.76 minutes, 24 events) had the highest mean duration and number of sighting events throughout the year, whilst February and

March (0 minutes, 0 events) had the lowest. Three significant peaks in number of peak events occur in May, June and November and January, these five months contain 78.76% of all peak sighting events. This is matched by a peak in mean duration from November to January which accounts for 52.56% of duration of peak events throughout the year (Supplementary figure S10).

The pattern of *M.alfredi* abundance gradually increases reaching its peak between 09:00 and 10:00 before decreasing. A secondary peak can be seen between 13:00 and 14:00, this decreases as the day continues. Around 56% of manta rays were observed over 5 hours of the day between the two peaks (09:00 to 14:00). From 17:00 onwards observations quickly diminished before the daily recording stopped (Supplementary Figure S11).

#### Site affiliation

Through photo identification 255 of the 1004 estimated manta ray sightings were confirmed. This was an assumed outcome, *M.alfredi* are cryptic in nature, to acquire a good identification, the individual would have to swim close to the camera and be positioned well within the field of view. Individuals were often observed in the distance, which could be additionally obscured by ocean conditions such as poor visibility, body position to camera and flora and fauna. A total of 57 individuals were identified from the 255 confirmed sightings. Out of the 57 identified, 40 were observed to repeatedly revisit, whilst 17 of these individuals visited the cleaning station once (Supplementary Figure S12).

Of the 40 individuals that were found to revisit the cleaning station, 61.40% were found to display site-fidelic behaviour, visiting the cleaning station throughout different months. The months with the greatest number of identified individuals that revisited per month were June 2021 (n=19), January 2022 (n=9), and May 2022 (n=9). Mantas MV-MA-2410, MV-MA-

2551, MV-MA-2913, MV-MA-3004 displayed the highest site fidelity, seen throughout a total of 8 months (Supplementary Figure S13). Manta MV-MA-2927 revisited the greatest number of times during a month, total of 6 times during June. There were 7 manta rays that visited the cleaning station  $\geq 10$  times over the year, Michele (MV-MA-2551) was the most sighted individual at 18 sightings (Figure 19b). The highest number of *M. alfredi* recorded at shallow block occurred on the 16/01/2022, an estimated total of 22 individuals were observed.

### Sex and Maturity Status

The overall sex ratio over the year was 55.29% female, 44.71% males; 141 females; 114 males. The month of May attracted the highest number of Female sightings (46) and Male sightings (35). Only February, April and July saw larger numbers of male sightings; whilst no males were recorded to visit in September (Supplementary Figure S14a). The overall maturity ratio was 61.96% adults, 55.29% juveniles, 0.39% subadult: 158 Adults, 96 Juveniles, 1 Subadult. However, only 57 individuals were identified throughout all deployments. May attracted the highest numbers of adult (54) and juvenile (26) sightings, featuring the only subadult of the year. A total of eight months were dominated by adults, whilst the remaining four months (February, August, September, December) consisted of more juveniles (Supplementary Figure S14b).

## Discussion

### Influence of environmental factors

#### Moon Phase

Moon phase was not found to be a probable predictor of manta abundance (MaxN) or presence. Moon phases have been seen to affect different sites in alternative manners, it is possible that they are not a primary driver within Hithadhoo Corner (Clark, 2010). The largest mean MaxN values were observed during first and third quarter phases, compounding findings from Jaine et al., 2012, which found higher sightings of cleaning manta rays during first and third quarters, and cruising individuals during the full moon. The largest peak in abundance during this study occurred during a full moon, it is likely individuals pass through the area to use the cleaning station for protection as a strategy to avoid visual predation during periods of increased irradiance (Braun et al., 2014). Whilst providing favourable cleaning conditions for the enhanced need for cleaning after mass feeding events; a common cause of cleaning station presence (Kruger, 2020). On the other hand, Barr and Abelson, 2019 suggested that manta rays were notably absent from cleaning stations during periods when the moon was more than half full, as under these conditions light intensity is high, causing large planktonic aggregations, triggering manta foraging behaviour and absence from cleaning stations (Clark, 2010; Armstrong et al., 2016).

It is likely that areas near to Hithadhoo Corner provide favourable feeding conditions during Full and New Moon (Kruger, 2020). Furthermore, large downward migrations of zooplankton are triggered by high intensities of moonlight, which consequently triggers longer periods of night-time diving by *M. alfredi* and absence from cleaning stations (Webster et al., 2015). However, feeding behaviour is not well documented in Laamu and is not a very common event at Hithadhoo Corner; only detected three times between 2019 and 2020 at Mendhoo (Sawers,



*pers comms*; Manta Trust, 2017; Manta Trust, 2020). Current nearby feeding locations are unknown, however are likely to be located on the down-current edges of the atoll during the southwest monsoon (Manta Trust, 2017). Visiting cleaning stations under low light conditions (First and Third Quarter) when foraging will be less efficient, would be beneficial for *M.alfredi* (Barr and Abelson, 2019). This again corresponds with our findings of differences in abundance between phases of increased irradiance and low light conditions. It is probable that the effect of moon phases would be found to be stronger if manta ray activity was surveyed during the night, many studies suggest the influence of moon on *M.alfredi* is dominated by strength of lunar illumination (Jaine et al., 2012; Rohner et al., 2013; Braun et al., 2014). Future studies should aim to collate data on this to identify a more concrete trend within the moon's influence.

#### Tidal Phase

This study shows no significant effect of tidal phase on *M.alfredi* abundance or presence at cleaning stations. Previous studies show that cleaning behaviour is mostly observed at and after high tide, especially during spring tides, when tidal exchange and water intensity is greatest (O'Shea et al. 2010, Jaine et al. 2012, Couturier et al. 2018; Peel et al., 2019). However, it is also shown that there can be strong tidal influence on manta ray presence during an ebb tide particularly in Raa Atoll; individuals move towards cleaning stations during this period due to favourable cleaning conditions and less favourable foraging conditions, this is a similar case for this study (O'Shea et al., 2010; ; Jaine et al., 2012; Armstrong et al., 2016; Manta Trust, 2019c; Harris and Stevens, 2021). Our results show that the highest abundance occurs at low tide, as high tide presents optimal feeding potential away from cleaning stations. Previous studies finding strong interactions between high tidal flux and manta presence which have attributed to increased prey availability (Dewar et al., 2008; Clark, 2010). Jaine et al., 2012 found increased sightings of *M.alfredi* in key feeding sites, peaking within the first few hours

of the ebb tide. This study produced similar results; abundance decreased 2 hours before high tide, revealing a potential optimal movement time towards feeding sites within the area; as a response to strong tidal currents that induce upwelling of deep water through Bernoulli suction, providing concentrated streams of plankton to atoll channels (Anderson et al., 2011b).

Larger tidal range is associated with increased *M.alfredi* detectability, tidal range within Hithadhoo varies in size, it is likely the lack of a significant tidal effect is due to small tidal ranges and lack of strong tidal currents necessary to drive upwelling events; as found to be the case in areas around Hawai'i, furthermore the strength of tidal effect on abundance varied within the Komodo islands (Dewar et al., 2008 ; Clark et al., 2010; Jaine et al., 2012; Harris and Stevens, 2021). In addition, O'Shea et al., 2010 suggests that outgoing tides from lagoon waters near cleaning stations are low in productivity, allowing manta rays to clean and conserve energy without sacrificing foraging opportunities (Nicholson-Jack et al., 2021). Further work is needed to investigate whether the main cause of inshore productivity in Hithadhoo Corner is the result of mesoscale eddies and island upwelling alongside local winds and islands topography that concentrate plankton in certain areas (Clark, 2010).

Although this study found no significant effect of tidal phase, many others have found the opposite, it is likely tidal phase is a small contributor to a larger system (O'Shea et al., 2010; Jaine et al., 2012; Krüger, 2020). The study of zooplankton concentrations within the Hithadhoo Channel would allow for a greater understanding of tidal phase and *M.alfredi* interactions. Tidal currents interacting with steep reef walls may accumulate plankton, this has been seen to occur at manta aggregation sites (Clark, 2010; Armstrong et al., 2016).

## Temperature

Temperature had a significant effect on both *M. alfredi* abundance and presence during this study, this effect was also found by Rohner et al., 2013. The study site showed constant temperatures throughout the year but was accompanied by large variations. Basking in warmer waters at cleaning stations particularly during the northeast monsoon season, allows manta rays to thermoregulate their endothermic bodies to favourable temperatures to augment their physiological functions to prepare for and recover metabolic costs incurred from deep diving or offshore forays (Hight and Lowe, 2007; Jirik and Lowe, 2012; Braun et al., 2014; Thorrold et al., 2014; Nicholson-Jack et al., 2021). Variation over the months of the northeast monsoon season, December and January experienced the higher number of individuals and larger MaxN (3) compared to February and March, where abundance and MaxN (1) was significantly reduced. A rise of temperatures from mid-January to the end of March provides a plausible reason for this. During the northeast monsoon there tends to be a drop in productivity and an average temperature increase of 3°C (Dewar et al., 2008). It is during this period a temperature increase by ~3°C is seen within our results; however, it is accompanied by variation and gradual decrease in manta abundance and time spent at the cleaning station. Within this study temperatures reached 30°C, which is considered as the maximum preferred threshold for manta rays, manta rays were seen to tolerate this temperature but for a reduced amount of time (Dewar et al., 2008). In addition, *M. alfredi* aggregate when sea surface temperatures may limit thermal and/or productive habitat along the species migration path (Couturier et al., 2018). Temperature is recognised as an important factor that affects elasmobranch feeding and reproduction (Dewar et al., 2008). Results suggest increased association between temperature and manta ray presence at cleaning stations, a result of thermoregulatory advantages gained by individuals, especially females occupying warm-water to reduce gestation times (Nicholson-Jack et al.,

2021). This explains why in-part we found higher concentrations of females throughout months with temperatures between the 29- 30°C.

### Influence of human presence

Pressures originating from tourism will only increase; between 2008 and 2018 the number of visitors to the Maldives more than doubled, significantly compounding pressures at key aggregation sites which could drive individuals away, reducing intra-species interaction, fecundity, fitness, and survivorship (Venables et al., 2016a). Murray et al., 2019 found that *M. alfredi* would abandon feeding behaviour when near humans. As a result, breeding success would dramatically decline as a result of displacement from cleaning stations, an important focal site for courtship and reproductive activity (Stevens 2018; Harris et al., 2020). However, this study was undertaken in Baa Atoll, where human-manta interactions are conducted via snorkelling, with higher densities of both parties. As the cleaning stations of Hithadhoo Corner are only reachable by experienced divers due to the depth of the location (15m – 22m), human-manta interactions occur often but in smaller numbers and hence aren't as affected; previous human disturbance within Hithadhoo Corner has been noted as low (Manta Trust, 2018). Nevertheless, although negative response to human interaction is short-term, disturbance is cumulative with the potential to incrementally develop into a significant issue (Venables et al., 2016a). Whilst tourism may act as a deterrent within the Maldives it remains definitive as to how and how much of an effect human interaction causes; the shift to tourism from fishing as a source of economic gain has benefitted the species (Anderson et al., 2011; Lynam, 2012; Venables et al., 2016a). Results from previous studies show that most interactions between humans and manta rays have largely been passive in nature (Atkins, 2011; Lynam, 2012). Lynam, 2012 found there was no response in almost 58% of recorded interactions, similar results from Atkins, 2011 and this study revealed relevant consistency in the behaviour of both

humans and manta rays, suggesting that tourists act responsibly during in-water encounters, limiting disturbance to *M.alfredi* (Lynam, 2012).

Manta rays are less disturbed at cleaning stations than at feeding aggregations, which supports our results (Lynam, 2012). This can be attributed to well-communicated briefings by resort dive operators and the Manta Trust team. As data from this study was collated as photographs, we were unable to assess change in behaviours to presence of humans. *M.alfredi* are understood to have some level of habituation to humans, with a primary reaction of no response, some manta rays redirect their course but did not display discomfort (King and Heinen, 2004; Lynam, 2012). Nevertheless, observed behavioural changes may mask unseen physiological responses (Lusseau and Bedjer, 2007). Another possible explanation for lack of affect, is that *M.alfredi* prioritise behaviours critical for maintaining their health over response to humans, this is often discussed between researchers (Lynam, 2012, Stevens, 2016). This is partially supported by this study's results, three months encountering >10 humans feature the largest MaxN 3 and average encounter times over 35 minutes. It must be considered the number of humans observed during this study were through the remote camera system at a singular cleaning station. Dive trips occur up to twice a day across all five of the cleaning stations at Hithadhoo Corner, future study could investigate the dive trip record data to acquire a higher resolution of the density and frequency of humans present at the site.

## Behavioural Patterns – Visitation, Site affiliation & Status

### Visitation

Visitation patterns at the site show that individuals were detected at the site between 09:00 – 14:00. Previous studies provide similar results, *M.alfredi* is predominantly detected during the day (Jaine et al., 2012; Peel et al., 2019). The peak time of detection between 09:00 – 10:00 was also found by Kruger, 2020 using the EOTR system in Baa Atoll. This morning time is

seen as a preference as the best time to clean in response to feeding at night, returning to the cleaning stations to be cleaned of residual matter (Gibson et al., 2011; Jaime et al., 2012; Couturier et al., 2018; Kruger, 2020). These peaks continued despite the presence of humans due to the operation of two consistent dives per day at the cleaning station during prime times of manta abundance. Variation within manta abundance in the morning could be a result of a change in plankton location; there are therefore less individuals during the evening that take more time to return to the cleaning station in the morning (Kruger, 2020). Setyawan et al., 2018 found the same patterns of temporal movement, *M. alfredi* present throughout the day, moving away offshore during the night as a foraging tactic to feed on the planktonic deep scattering layer (Dewar et al., 2008). Further investigation of night-time manta ray movements is needed to confirm this hypothesis, as it is unexplored within this study.

Frequentation of the site during the day may be associated with the fact that cleaner fish are only active during daylight hours (Harris and Stevens, 2021). Cleaner fish are affected by hydrodynamic processes such as temperature, which may impair cleaning performance, causing the manta client to leave (Barr and Abelson, 2019). Decreases in manta ray presence near the end of the day could be explained by reduction in cleaner fish activity. However, it has been found that the function of cleaning and parasite removal may be a secondary or tertiary driver of site use, with social and sexual interactions taking precedence (Stevens, 2016). These supports results found as mean encounter time significantly affected MaxN, with both variables increasing together. The highest average MaxN and encounter time occurred at either the beginning or the turn of the southwest and northeast Monsoon. These times of year provide favourable conditions, changes in winds drive upwellings of nutrient-rich waters, promoting ecosystem productivity (Anderson et al., 2011). Nevertheless, months with higher abundance

sightings could be a result of non-breeding social aggregations as individuals choose to group with preferred social partners each year (O'Shea et al., 2010; Perryman et al., 2019).

#### Site affiliation

Manta rays that visited during multiple months tended to also have a higher record of number of visits to the site (MV-MA-2551; 2900; 2913; 3004; 3754). This high utilisation alongside regular and repeated sighting of individuals suggests that *M. alfredi* have a level of fidelity to Hithadhoo Corner (Harris and Stevens, 2021). This supports long-term evidence that site fidelity is a well-known characteristic of *M. alfredi*, but can vary between individuals; this is evident from our results which show 29.82% of identified individuals were sighted only once (Braun et al., 2014; Stevens, 2016). Further to this, individuals that visited frequently but not over multiple months are presumed to be present during a period of favourable conditions and larger aggregation months. Harris and Stevens, 2021 hypothesised how each individual seasonally inhabits a home range, exploiting this area for resources before migrating to a secondary home range with the change in monsoon season. The combination of site fidelity and single encounters in this study supports this hypothesis; individuals sighted once may inhabit another home range, whether within Laamu Atoll or surrounding atolls. Laamu experiences strong oceanic currents, however water movement is limited, and no clear seasonal migration pattern has been documented (Manta Trust, 2020). Site fidelity is found to vary between areas, high fidelity in some years, seasonal fidelity in others (Clark, 2010). Our findings show potential for a high degree of plasticity of manta ray movement patterns, some of the newer less frequent individuals could utilise different locations, such as Fushi Kandu (in the northeast of Laamu) which like Hithadhoo Corner, is most active during the southwest monsoon (Manta Trust *pers comms*). However, alternative sites and tracking of individuals will need to be investigated to confirm this hypothesis. The population is noted to be small but

highly resident, few individuals are known to other atolls (Manta Trust, 2020). This small home range, as represented by the population's behaviour would benefit from localised, targeted protective management (Manta Trust, 2017).

### Sex & Maturity Status

Results suggest that visitation patterns could be associated with habitat use between different sex and maturity levels (Harris and Stevens, 2021). At the cleaning station, both females and mature individuals were frequently sighted over male and juvenile individual counterparts, this is a consistent occurrence at this site between 2018-2020 (Manta Trust, 2020). Historically, Hithadhoo Corner has supported year-round sightings with peaks at the start of southwest monsoon. The largest number of individuals and peak sighting events occurred during this period, productivity peaks near the end of the southwest monsoon often coincide with reproduction (Manta Trust, 2020; Manta Trust, 2019a; Manta Trust, 2018; Manta Trust, 2017; Manta Trust, 2016).

Within eight of the months studied, maturity status influenced visitation frequency; there were higher numbers of adults than juveniles (Stevens, 2016). Finding a mate is a main driver at cleaning stations, which could explain reduced site visitation of juveniles who have different requirements, prioritising refuge provide by cleaning stations from predatory attacks (Stevens, 2016). However, cleaning stations are often found in channels, which are exposed and provide higher threats of predatory attacks that are not favourable for juveniles but can be tolerated by adults (Tam Sawers, *pers comms*, Strike et al., 2022).

Adult females are known to dominate cleaning stations, the intensity of cleaning station philopatry could be linked to mate-seeking behaviour, sexually mature females frequent sites with cleaning opportunities, food availability and safety, whereas males travel to various sites



in search of females (Deakos et al., 2011; Bleu et al., 2012; Jacoby et al., 2012; Stevens, 2016; Harris and Stevens 2021). Individual manta ray resighting events were highest during the turn of the monsoons (May-June; October-November) when courtship activity is known to occur. Sites will switch to male-dominated during courtship season, however, we found no data to support this, suggesting that currently this is a site where little courtship is displayed; this has been the case between 2019-2022 (Stevens, 2016). The most philopatric manta rays were equally male and female, therefore it is unlikely variation in site visitation is attributed to habitat use by sex (Harris and Stevens, 2021). However, prior to this, Hithadhoo Corner was known for manta ray courtship, 10 pregnant individuals were recorded in 2017 (Manta Trust, 2020; Manta Trust, 2019; Manta Trust, 2018; Manta Trust, 2017). Studies in Baa Atoll have suggested that this decrease could be a result of a lack of food brought about by the weakened monsoons (Manta Trust, 2017). Variation over the past 5 years in reproductive behaviour shows highly variable fecundity and an overall slow reproductive rate. Females can store sperm as a strategy to ensure offspring are born at a time with favourable conditions to allow for the best chances of survival (Manta Trust, 2017).

### Recommendations for Hithadhoo Channel Protected Area

Previous stakeholder and tourism survey responses have highlighted the importance of manta rays to local tourism, emphasising the need for increased protection through the implementation of strongly enforced MPAs (Venables et al., 2016b). Currently, limited numbers of manta ray aggregation sites fall within MPAs with active enforcement; with a highly philopatric population in Laamu, and the predictable utilisation of Hithadhoo Corner as key aggregation site, suggests increased environmental influence. It is highly recommended that Hithadhoo Corner is included within the Hithadhoo Channel Protected Area. Having identified this area as an important area of use, future conservation decisions can be effectively focused (Harris et al., 2020). The provision of a regional-scale population management strategy

and a decision to designate the Hithadhoo Channel Protected Area as a ‘no-take’ zone, would protect *M.alfredi* from propeller injuries and strikes from local and tourist boats; a common and major concern for the Maldivian subpopulation (Stewart and Jaine et al., 2018; Peel et al. 2019). A reduction in fishing activity will also allow further regenerative recovery of the reef ecosystem and cleaning stations. Further to this, a buffer zone around the protected area to further protect individuals moving between the open ocean and cleaning stations.

Protection of critical habitats such as aggregation sites are essential for the species survival, yet a suitable balance between environmental, economic, and socio-cultural aspects needs to be reached (Clark, 2010; Hani et al., 2019). With many ‘live-aboard’ surf and dive excursion boats frequenting the area, regulating tourism through the strong enforcement of a code-of-conduct within the protected area is essential for future ecological and financial success (Harris et al., 2020). A 10-step guide on how to swim with manta rays and a code-of-conduct was published by The Manta Trust in 2017, to mitigate the impacts of tourism (<https://swimwithmantas.org/>) (Muarry et al., 2019; Manta Trust, 2021). This is already used successfully by operations that run from Six Senses Laamu and would be wise for all other operators and fishers within the area to receive this.

Training of a ranger team could be modelled on the success of enforcement across the Baa Atoll Biosphere Reserve, of which the Maldivian Environmental Protection Agency and IUCN have been previously involved with (Maldives Insider, 2017; Manta Trust, 2019b). Due to high use of the area, Six Senses Laamu could contribute towards the funding of this through the resort’s sustainability fund. After the success of enforcement in Ningaloo Marine Park, Australia, Venables et al., 2016 recommends the use of similar precautionary management strategies for *M.alfredi* (Harris et al., 2020). These strategies use anticipatory measures which

aim to integrate the protection of people and environment against anthropogenic threats (UNESCO, 2005; DPaW, 2013). Manta ray ecotourism can involve local communities through employment and capital investment (Hani et al., 2019). Effectiveness of local-scale management is exemplified by Raja Ampat Shark and Ray Sanctuary, with a track-record of self-enforcement and community engagement (Stewart et al., 2016). The requirement enforcing licences for operators with strict conditions to mitigate the harm of *M.alfredi* is an example of a regulation that would aid in minimising disturbance (Harris et al., 2020). Further annual data can be used to advise seasonal restrictions of activities within the area during periods of importance and inform predictions on when alternative cleaning station habitats are most vital to the health of manta populations.

### Limitations & Future Study

The current study was limited by the inclusion of just one of the cleaning stations within Hithadhoo Corner and as a result potentially sampled only a section of the areas' population demographic. Additionally, missing data values restricted the conclusion of the effect of temperature, future studies should take this into account.

Previous observation studies have provided quantitative evidence that *M.alfredi* migrates east-west and west-east biannually, following concentrations of plankton (Anderson et al., 2011; Kitchen-Wheeler et al., 2011; Harris et al., 2020). To further this study, research within the area could help identify the essential requirements needed for successful *M.alfredi* fitness and reproductive success (Harris et al., 2020). Comparative studies over the Maldives could highlight additional areas that are crucial for the survival of this sub-population. Which could eventually allow for the expansion of Laamu Atoll's protected area network to encompass additional key aggregation sites, the identification and protection of migration corridors will

further strengthen the future of this sub-population. With climate change influencing range-shifts in elasmobranch species and weakening the southwest monsoon, an integrated approach accounting for the effect of environmental variables on *M.alfredi* behaviours within future RCP climate scenarios will facilitate contingency planning within the management strategies of existing and future protected areas (Schlaff et al., 2014; Wheeler et al., 2020).

## Conclusion

This year-long study on an isolated and unfished population of *M.alfredi* in the south of Laamu Atoll, serves as a baseline assessment providing insight towards the characterised environmental drivers of cleaning station use, association with humans and the resultant behaviours. Remote camera systems prove a useful tool to collect long-term data without the bias of human presence allowing us to ultimately elucidate current knowledge of the manta rays of Laamu Atoll. We successfully highlighted key times of the year where sightings are likely, this knowledge is especially important to inform stakeholders who use the area. Results indicate higher abundances of *M.alfredi* at cleaning stations when environmental conditions are favourable, it was also presumed that increased presence was a result of enhanced need of cleaning after mass feeding events; temperature was a key driver of this. However, abundance may be independent from environmental cues and human presence; cleaning may only be a secondary or tertiary driver of abundance as social occurrences may take precedence of influencing aggregations of *M.alfredi*. It is essential the correct steps are taken when creating management decisions within Hithadhoo. The implementation of recommendations of this study shall aid in securing the future of Laamu's part of the *M.alfredi* Maldivian sub-population.

## Acknowledgements

This Master's Thesis was only possible with the great support and teachings of my supervisors Phil Doherty and Jas Corbett. I would like to thank Phil for his constant support throughout the project and Jas for taking me under her wing at the Manta Trust and teaching me about all things manta! It has been a truly amazing experience and I could not be grateful enough for the opportunity to undertake this project. I also thank the Maldives Underwater Initiative team: Ali, Miri, Greg, Jake, Affaz, Mufliha, Jinnad,, Afra, Leanna, Yamyn and Ish, for such a welcome, friendship and their knowledge throughout my stay at Six Senses Laamu. A thank you to Julie Hawkins, for all her efforts in organising my trip to the Maldives.

Thank you to my family, in particular my mother Amanda, father John and brother Alexander for their constant support throughout my degree, and for encouraging me not to settle for a desk job!

To the Maldivian Meteorological Society for providing much needed historical data on the tides of Laamu. Funding was provided by the University of Exeter and the Manta Trust, without this, the project would not have been possible. I am forever grateful for the opportunities provided to myself and other students as part of this degree.

## References

Anderson, R.C., Adam, M.S. and Goes, J.I., (2011a). From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives. *Fisheries Oceanography*, 20(2), pp.104-113.

Anderson, R.C., Adam, M.S., Kitchen-Wheeler, A.M. and Stevens, G., (2011b). Extent and economic value of manta ray watching in Maldives. *Tourism in Marine Environments*, 7(1), pp.15-27.

Armstrong, A.O., Armstrong, A.J., Jaine, F.R., Couturier, L.I., Fiora, K., Uribe-Palomino, J., Weeks, S.J., Townsend, K.A., Bennett, M.B. and Richardson, A.J., 2016. Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the Great Barrier Reef. *PloS one*, 11(5), p.e0153393.

Armstrong, A.J., Armstrong, A.O., Bennett, M.B., McGregor, F., Abrantes, K.G., Barnett, A., Richardson, A.J., Townsend, K.A. and Dudgeon, C.L., 2020. The geographic distribution of reef and oceanic manta rays (*Mobula alfredi* and *Mobula birostris*) in Australian coastal waters. *Journal of Fish Biology*, 96(3), pp.835-840.

Armstrong, A.O., Stevens, G.M., Townsend, K.A., Murray, A., Bennett, M.B., Armstrong, A.J., Uribe-Palomino, J., Hosegood, P., Dudgeon, C.L. and Richardson, A.J., 2021. Reef manta rays forage on tidally driven, high density zooplankton patches in Hanifaru Bay, Maldives. *PeerJ*, 9, p.e11992.

Ashok, K., Guan, Z. & Yamagata, T., 2001. Impact of the Indian Ocean Dipole on the Relationship between the Indian Monsoon Rainfall and ENSO. *Geophysical Research Letters*, 28(23), pp.4499–4502.

Aslam, M. and Kench, P.S., 2017. Reef island dynamics and mechanisms of change in Huvadhu Atoll, Republic of Maldives, Indian Ocean. *Anthropocene*, 18, pp.57-68.

Atkins, B. Manta Ray (*Manta alfredi*) Tourism in Baa Atoll, Republic of Maldives: Human Interactions, Behavioural Impacts and Management Implications. (Masters Thesis, University of York)

Bansemer, C.S. and Bennett, M.B., 2010. Retained fishing gear and associated injuries in the east Australian grey nurse sharks (*Carcharias taurus*): implications for population recovery. *Marine and Freshwater Research*, 61(1), pp.97-103.

Barr, Y. and Abelson, A., 2019. Feeding–Cleaning Trade-Off: Manta Ray “Decision-Making” as a Conservation Tool. *Frontiers in Marine Science*, 6, p.88.

Bleu, J., Bessa-Gomes, C. & Laloi, D., 2012. Evolution of female choosiness and mating frequency: Effects of mating cost, density, and sex ratio. *Animal Behaviour*, 83(1), pp.131–136.

Braun, C.D., Skomal, G.B., Thorrold, S.R. and Berumen, M.L., 2014. Diving behaviour of the reef manta ray links coral reefs with adjacent deep pelagic habitats. *PloS one*, 9(2), p.e88170.

Braun, C.D., Skomal, G.B., Thorrold, S.R. & Berumen, M.L., 2015. Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. 179 *Marine Biology*, pp.1–12.

Byrne, M., 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. In R. N. Gibson, R. J. A. Atkinson, & J. D. M. Gordon, eds. *Oceanography and Marine Biology*. CRC Press, pp. 1–42.

Campbell, M.D., Pollack, A.G., Gledhill, C.T., Switzer, T.S. and DeVries, D.A., 2015. Comparison of relative abundance indices calculated from two methods of generating video count data. *Fisheries Research*, 170, pp.125-133.

Campbell, M.D., Salisbury, J., Caillouet, R., Driggers, W.B. and Kilfoil, J., 2018. Camera field-of-view and fish abundance estimation: A comparison of individual-based model output and empirical data. *Journal of Experimental Marine Biology and Ecology*, 501, pp.46-53.

Cheney, K.L. & Côté, I.M., 2005. Mutualism or parasitism? The variable outcome of cleaning symbioses. *Biology letters*, 1(2), pp.162–5.

Clark, T.B., 2010. Abundance, home range, and movement patterns of manta rays (*Manta alfredi*, *M. birostris*) in Hawaii. University of Hawaii, Manoa.



Cisneros-Montemayor, A.M. and Sumaila, U.R., 2010. A global estimate of benefits from ecosystem-based marine recreation: potential impacts and implications for management. *Journal of Bioeconomics*, 12(3), pp.245-268.

Colton, M.A. and Swearer, S.E., 2010. A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. *Marine Ecology Progress Series*, 400, pp.19-36.

Couturier, L.I.E., Dudgeon, C.L., Pollock, K.H., Jaine, F.R.A., Bennett, M.B., Townsend, K.A., Weeks, S.J. & Richardson, A.J., 2014. Population dynamics of the reef manta ray *Manta alfredi* in eastern Australia. *Coral Reefs*, 33, pp.329–342.

Couturier, L.I., Jaine, F.R., Townsend, K.A., Weeks, S.J., Richardson, A.J. and Bennett, M.B., 2011. Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Krefft, 1868), along the east coast of Australia. *Marine and Freshwater Research*, 62(6), pp.628-637.

Couturier, L.I.E., Marshall, A.D., Jaine, F.R.A., Kashiwagi, T., Pierce, S.J., Townsend, K.A., Weeks, S.J., Bennett, M.B. and Richardson, A.J., 2012. Biology, ecology, and conservation of the Mobulidae. *Journal of fish biology*, 80(5), pp.1075-1119.

Couturier, L.I.E., Newman, P., Jaine, F.R.A., Bennett, M.B., Venables, W.N., Cagua, E.F., Townsend, K.A., Weeks, S.J. and Richardson, A.J., 2018. Variation in occupancy and habitat use of *Mobula alfredi* at a major aggregation site. *Marine Ecology Progress Series*, 599, pp.125-145.

Croll, D.A., Dewar, H., Dulvy, N.K., Fernando, D., Francis, M.P., Galván-Magaña, F., Hall, M., Heinrichs, S., Marshall, A., McCauley, D. and Newton, K.M., 2016. Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. *Aquatic conservation: marine and freshwater ecosystems*, 26(3), pp.562-575.

Deakos, M.H., (2011a). The reproductive ecology of resident manta rays (*Manta alfredi*) off Maui, Hawaii, with an emphasis on body size. *Environmental Biology of Fishes*, 94(2), pp.1–14.

Deakos, M.H., Baker, J.D. and Bejder, L., (2011b). Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. *Marine Ecology Progress Series*, 429, pp.245-260.

Deik, H., Reuning, L. and Pfeiffer, M., 2017. Orbital scale variation of primary productivity in the central equatorial Indian Ocean (Maldives) during the early Pliocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 480, pp.33-41.

Department of Parks and Wildlife (DPaW), 2013. Whale shark management with particular reference to Ningaloo Marine Park. *Western Australia wildlife management plan no. 57*.

Dewar, H., Mous, P., Domeier, M., Muljadi, A., Pet, J. & Whitty, J., 2008. Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Marine Biology*, 155(2), pp.121–133.

Dulvy, N.K. et al., 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18, pp.459–482.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P. and Pollock, C.M., (2014a). Extinction risk and conservation of the world's sharks and rays. *elife*, 3, p.e00590.

Dulvy, N.K., Pardo, S.A., Simpfendorfer, C.A. and Carlson, J.K., (2014b). Diagnosing the dangerous demography of manta rays using life history theory. *PeerJ*, 2, p.e400.

Dulvy, N.K., Sadovy, Y. & Reynolds, J.D., 2003. Extinction vulnerability in marine populations. *Fish and Fisheries*, 4(1), pp.25–64.

EPA, M., 2014. Batoidea Maldives Protection Gazette No.(IUL) 438-ECAS.

Fernando, D. and Stewart, J.D., 2021. High bycatch rates of manta and devil rays in the “small-scale” artisanal fisheries of Sri Lanka. *PeerJ*, 9, p.e11994.

Freedman, R., Roy, S., 2012. Spatial patterning of *Manta birostris* in United States east coast offshore habitat. *Applied Geography* 32, 2: 652-659.

Frisk, M.G., 2010. Life History Strategies of Batoids. In J. C. Carrier, J. A. Musick, & M. R. Heithaus, eds. *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*. CRC Press, pp. 283–307.51 187

Frisk, M.G., Miller, T.J. & Dulvy, N.K., 2005. Life histories and vulnerability to exploitation of elasmobranchs: Inferences from elasticity, perturbation, and phylogenetic analyses. *Journal of Northwest Atlantic Fishery Science*, 35(October), pp.27–45.

Gadig, O.B.F. & Neto, D.G., 2014. Notes on the feeding behaviour and swimming pattern of *Manta alfredi* (Chondrichthyes, Mobulidae) in the Red Sea. *Acta Ethologica*, 17(2), pp.119–122.

Garrod, B. and Wilson, J.C., 2004. Nature on the edge? Marine ecotourism in peripheral coastal areas. *Journal of sustainable tourism*, 12(2), pp.95-120.

Gibson, R., Atkinson, R., Gordon, J., Smith, I. and Hughes, D., 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanography Marine Biology Annual Review*, 49, pp.1-42.

Gischler, E., Storz, D. & Schmitt, D., 2014. Sizes, shapes, and patterns of coral reefs in the Maldives, Indian Ocean: the influence of wind, storms, and precipitation on a major tropical carbonate platform. *Carbonates and Evaporites*, 29(1), pp.73–87.

Graham, R.T., Witt, M.J., Castellanos, D.W., Remolina, F., Maxwell, S., Godley, B.J. and Hawkes, L.A., 2012. Satellite tracking of manta rays highlights challenges to their conservation. *PloS one*, 7(5), p.e36834.

Hani, M.S., Jompa, J., Nessa, M.N. and White, A.T., 2019, April. Manta ray watching tourism in Eastern Indonesia: Is it sustainable?. In *IOP Conference Series: Earth and Environmental Science* (Vol. 253, No. 1, p. 012042). IOP Publishing.

Harris, J.L., Hosegood, P., Robinson, E., Embling, C.B., Hilbourne, S. and Stevens, G.M., 2021. Fine-scale oceanographic drivers of reef manta ray (*Mobula alfredi*) visitation patterns at a feeding aggregation site. *Ecology and evolution*, *11*(9), pp.4588-4604.

Harris, J.L., McGregor, P.K., Oates, Y. and Stevens, G.M., 2020. Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (*Mobula alfredi*) in the Maldives, implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *30*(8), pp.1649-1664.

Harris, J.L. and Stevens, G.M., 2021. Environmental drivers of reef manta ray (*Mobula alfredi*) visitation patterns to key aggregation habitats in the Maldives. *PloS one*, *16*(6), p.e0252470.

Hartig, F. 2016. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1. 0. [CRAN](#) / [GitHub](#)

Harvey, E.S., Cappel, M., Butler, J.J., Hall, N., and Kendrick, G.A., 2007. Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. *Marine Ecology Progress Series*, *350*, pp.245-254.

HDX. 2021. *Maldives - Subnational Administrative Boundaries*. [online] Available at: <<https://data.humdata.org/dataset/cod-ab-mdv>> [Accessed 1 August 2022].

Heithaus, M.R., Frid, A., Wirsing, A.J. and Worm, B., 2008. Predicting ecological consequences of marine top predator declines. *Trends in ecology & evolution*, 23(4), pp.202-210.

Hight, B.V., Lowe, C.G., 2007. Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioural thermoregulation? *Journal of Experimental Marine Biology and Ecology*, 352(1), pp.114–128.

Hosegood, J., Humble, E., Ogden, R., de Bruyn, M., Creer, S., Stevens, G., Abudaya, M., Bassos-Hull, K., Bonfil, R., Fernando, D. and Foote, A.D., 2018. Phylogenomic and species delimitation of mobulid rays reveals cryptic diversity and a new species of manta ray. *bioRxiv*, p.458141.

Jacoby, D.M.P., Croft, D.P. & Sims, D.W., 2012. Social behaviour in sharks and rays: analysis, patterns, and implications for conservation. *Fish and Fisheries*, 13(4), pp.399–417.

Jaine, F.R., Couturier, L.I., Weeks, S.J., Townsend, K.A., Bennett, M.B., Fiora, K. and Richardson, A.J., 2012. When giants turn up: sighting trends, environmental influences, and habitat use of the manta ray *Manta alfredi* at a coral reef.

Jaine, F.R.A., Rohner, C.A., Weeks, S.J., Couturier, L.I.E., Bennett, M.B., Townsend, K.A. & Richardson, A.J., 2014. Movements and habitat use of reef manta rays off eastern Australia: offshore excursions, deep diving and eddy affinity revealed by satellite telemetry. *Marine Ecology Progress Series*, 510, pp.73–86.

Jirik, K.E., Lowe, C.G., 2012. An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. *Journal of Fish Biology*, 80(5), pp.1227–45.

Kashiwagi, T., Marshall, A.D., Bennett, M.B. and Ovenden, J.R., 2011. Habitat segregation and mosaic sympatry of the two species of manta ray in the Indian and Pacific Oceans: *Manta alfredi* and *M. birostris*. *Marine Biodiversity Records*, 4.

Kitchen-Wheeler, A.M., 2010. Visual identification of individual manta ray (*Manta alfredi*) in the Maldives Islands, Western Indian Ocean. *Marine Biology Research*, 6(4), pp.351-363.

Kitchen-Wheeler, A.M., Ari, C., and Edwards, A.J., 2012. Population estimates of Alfred mantas (*Manta alfredi*) in central Maldives atolls: North Male, Ari and Baa. *Environmental Biology of Fishes*, 93(4), pp.557-575.

Kessel, S.T., Elamin, N.A., Yurkowski, D.J., Chekchak, T., Walter, R.P., Klaus, R., Hill, G. and Hussey, N.E., 2017. Conservation of reef manta rays (*Manta alfredi*) in a UNESCO World Heritage Site: Large-scale Island development or sustainable tourism?. *PloS one*, 12(10), p.e0185419.

Krüger, L., 2020. *Using remote cameras to uncover the hidden habits of reef manta rays (Mobula alfredi) in the Maldives*. (Masters Thesis, University of Rostock).

Lassauce, H., Chateau, O., Erdmann, M.V. and Wantiez, L., 2020. Diving behaviour of the reef manta ray (*Mobula alfredi*) in New Caledonia: More frequent and deeper night-time diving to 672 meters. *Plos one*, 15(3), p.e0228815.

Lawson, J.M., Fordham, S.V., O'Malley, M.P., Davidson, L.N., Walls, R.H., Heupel, M.R., Stevens, G., Fernando, D., Budziak, A., Simpfendorfer, C.A. and Ender, I., 2016. Sympathy for the devil: a conservation strategy for devil and manta rays. *PeerJ*, 5, p.e3027.

Lynam, B. The Impacts of Tourism on a Population of Manta Rays, Baa Atoll, Republic of Maldives. (Masters Thesis)

Maldives Insider. 2017. *Ranger training programme in Baa atoll biosphere reserve concludes*. [online] Available at: <<https://maldives.net.mv/21155/ranger-training-programme-in-baa-atoll-biosphere-reserve-concludes/>> [Accessed 22 July 2022].

Mallet, D. and Pelletier, D., 2014. Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). *Fisheries Research*, 154, pp.44-62.

Manta Trust, 2016. *Annual Report Laamu Atoll 2016*. <https://www.mantatrust.org/resources/> Accessed: August, 2022.

Manta Trust, 2017. *Annual Report Laamu Atoll 2017*. <https://www.mantatrust.org/resources/> Accessed: August, 2022.



Manta Trust, 2018. *Annual Report Laamu Atoll 2018*. <https://www.mantatrust.org/resources/>  
Accessed: August, 2022.

Manta Trust, (2019a). *Annual Report Laamu Atoll 2019*.  
<https://www.mantatrust.org/resources/> Accessed: August, 2022.

Manta Trust, (2019b). *Annual Report Baa Atoll 2019*. <https://www.mantatrust.org/resources/>  
Accessed: August, 2022.

Manta Trust, (2019c). *Annual Report Raa Atoll 2019*. <https://www.mantatrust.org/resources/>  
Accessed: August, 2022.

Manta Trust, 2020. *Annual Report Laamu Atoll 2020*. <https://www.mantatrust.org/resources/>  
Accessed: August, 2022.

Manta Trust, 2021. *Impact Report - A summary of the Manta Trust's charitable research and conservation work in 2021*. [online] Corscombe: Manta Trust, pp.1-21. Available at:  
<[https://static1.squarespace.com/static/5a196500914e6b09132e911f/t/62299159ab79915c015260ce/1646891433196/Manta+Trust\\_Impact+Report\\_2021.pdf](https://static1.squarespace.com/static/5a196500914e6b09132e911f/t/62299159ab79915c015260ce/1646891433196/Manta+Trust_Impact+Report_2021.pdf)> [Accessed 20 June 2022].

Manta Trust, 2022. Conservation through Research, Education and Collaboration.  
<http://www.mantatrust.org/> Accessed: June, 2021.

Marshall, A.D. & Bennett, M.B., (2010a). Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. *Journal of Fish Biology*, 77(1), pp.169–90.

Marshall, A.D., Bennett, M.B., (2010b). The frequency and effect of shark-inflicted bite injuries to the reef manta ray *Manta alfredi*. *African Journal of Marine Science*, 32(3), pp.573–580.

Marshall, A., Kashiwagi, T., Bennett, M.B., Deakos, M., Stevens, G., McGregor, F., Sato, K. 2018. *Mobula alfredi*. *The IUCN Red List of Threatened Species*, 8235, 1-21.

McCauley, D.J., DeSalles, P.A., Young, H.S., Papastamatiou, Y.P., Caselle, J.E., Deakos, M.H., Gardner, J., Garton, D.W., Collen, J.D. and Micheli, F., 2014. Reliance of mobile species on sensitive habitats: a case study of manta rays (*Manta alfredi*) and lagoons. *Marine biology*, 161(9), pp.1987-1998.

Ministry of Environment, Climate Change and Technology, 2021. *Laamu Atoll Environmentally Protected Areas*. Male: Ministry of Environment, Climate Change and Technology, pp.1-14. Available at:< <http://www.environment.gov.mv/v2/en/download/13853>> [Accessed 9 May 2022].

Ministry of Tourism. 2016. Statistics, monthly updates. [Online] Retrieved from <http://www.tourism.gov.mv/statistics/arrival-updates/>

Mission Blue, 2021. *Laamu Atoll hope spot in Maldives highlights harmony between marine conservation and economic development*. [online] Available at: <<https://mission-blue.org/2021/10/laamu-atoll-hope-spot-in-maldives-highlights-harmony-between-marine-conservation-and-economic-development/>> [Accessed 9 May 2022].

Murray, A., Garrud, E., Ender, I., Lee-Brooks, K., Atkins, R., Lynam, R., Arnold, K., Roberts, C., Hawkins, J. and Stevens, G., 2019. Protecting the million-dollar mantas; creating an evidence-based code of conduct for manta ray tourism interactions. *Journal of Ecotourism*, 19(2), pp.132-147.

Nicholson-Jack, A.E., Harris, J.L., Ballard, K., Turner, K.M. and Stevens, G.M., 2021. A hitchhiker guide to manta rays: Patterns of association between *Mobula alfredi*, *M. birostris*, their symbionts, and other fishes in the Maldives. *PloS one*, 16(7), p.e0253704.

O'Malley, M.P., Lee-Brooks, K., and Medd, H.B., 2013. The global economic impact of manta ray watching tourism. *PloS one*, 8(5), p.e65051.

O'Malley, M.P., Townsend, K.A., Hilton, P., Heinrichs, S. and Stewart, J.D., 2017. Characterization of the trade in manta and devil ray gill plates in China and South-east Asia through trader surveys. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(2), pp.394-413.

O'Shea, O.R., Kingsford, M.J. and Seymour, J., 2010. Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef. *Marine and Freshwater Research*, 61(1), pp.65-73.

Peel, L.R., Stevens, G.M., Daly, R., Daly, C.A.K., Lea, J.S., Clarke, C.R., Collin, S.P. and Meekan, M.G., (2019a). Movement and residency patterns of reef manta rays *Mobula alfredi* in the Amirante Islands, Seychelles. *Marine Ecology Progress Series*, 621, pp.169-184.

Peel, L.R., Daly, R., Keating Daly, C.A., Stevens, G.M., Collin, S.P. and Meekan, M.G.,(2019b). Stable isotope analyses reveal unique trophic role of reef manta rays (*Mobula alfredi*) at a remote coral reef. *Royal Society open science*, 6(9), p.190599.

Peel, L.R., Stevens, G.M., Daly, R., Keating Daly, C.A., Collin, S.P., Nogués, J. and Meekan, M.G., 2020. Regional movements of reef manta rays (*Mobula alfredi*) in Seychelles waters. *Frontiers in Marine Science*, 7, p.558.

Perryman, R.J., Venables, S.K., Tapilatu, R.F., Marshall, A.D., Brown, C., and Franks, D.W., 2019. Social preferences and network structure in a population of reef manta rays. *Behavioral Ecology and Sociobiology*, 73(8), pp.1-18.

Powles, H., Bradford, M.J., Bradford, R.G., Doubleday, W.G., Innes, S. and Levings, C.D., 2000. Assessing and protecting endangered marine species. *ICES Journal of Marine Science*, 57(3), pp.669-676.

R Core Team., 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

Revolutionary GIS. 2017. *Maldives Shapefile Data*. [online] Available at: <<https://revolutionarygis.wordpress.com/tag/maldives-atoll-shapefile/>> [Accessed 1 August 2022].

Richardson, A.J., 2008. In hot water: zooplankton and climate change. *ICES Journal of Marine Science*, 65(3), pp.279-295.

Rohner, C.A., Pierce, S.J., Marshall, A.D., Weeks, S.J., Bennett, M.B. and Richardson, A.J., 2013. Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. *Marine Ecology Progress Series*, 482, pp.153-168.

Sasamal, S.K., 2006. Island mass effect around the Maldives during the winter months of 2003 and 2004. *International Journal of Remote Sensing*, 27(22), pp.5087-5093.

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. and Votier, S.C., 2014. On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51(6), pp.1575-1583.

Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2014. Influence of environmental factors on shark and ray movement, behaviour, and habitat use: a review. *Reviews in Fish Biology and Fisheries*, 24:1089- 1103.

Setyawan, E.D.Y., Erdmann, M.V., Lewis, S.A., Mambrasar, R., Hasan, A.W., Templeton, S., Beale, C.S., Sianipar, A.B., Shidqi, R., Heuschkel, H. and Ambafen, O., 2020. Natural history of manta rays in the Bird's Head Seascape, Indonesia, with an analysis of the demography and spatial ecology of *Mobula alfredi* (Elasmobranchii: Mobulidae). *J Ocean Sci Found*, pp.49-83.

Setyawan, E., Stevenson, B.C., Izuan, M., Constantine, R., and Erdmann, M.V., 2022. How Big Is That Manta Ray? A Novel and Non-Invasive Method for Measuring Reef Manta Rays Using Small Drones. *Drones*, 6(3), p.63.

Sherman, C.S., Chin, A., Heupel, M.R. and Simpfendorfer, C.A., 2018. Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics?. *Journal of Experimental Marine Biology and Ecology*, 503, pp.80-85.

Shima, J.S., Osenberg, C.W., Alonzo, S.H., Noonburg, E.G. and Swearer, S.E., 2022. How moonlight shapes environments, life histories, and ecological interactions on coral reefs. *Emerging Topics in Life Sciences*, 6(1), pp.45-56.

Stevens, G.M.W., 2016. *Conservation and population ecology of manta rays in the Maldives* (Doctoral dissertation, University of York).

Stevens, G., Dando, M., Fernando, D. and Notarbartolo di Sciara, G., 2018. *Guide to the Manta and Devil Rays of the World*. 1st ed. Plymouth: Wild Nature Press, pp.1-144.

Stevens, G.M. and Froman, N., 2019. The Maldives Archipelago. In *World seas: an environmental evaluation* (pp. 211-236). Academic Press.

Stevens, G.M., Hawkins, J.P., and Roberts, C.M., 2018. Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives. *Journal of Fish Biology*, 93(2), pp.344-359.

Stewart, J.D., Beale, C.S., Fernando, D., Sianipar, A.B., Burton, R.S., Semmens, B.X. & Aburto-Oropeza, O., 2016. Spatial Ecology and Conservation of *Manta birostris* in the Indo-Pacific. *Biological Conservation*, 200.

Stewart, J.D., Hoyos-Padilla, E.M., Kumli, K.R. & Rubin, R.D., 2016. Deep-water feeding and behavioral plasticity in *Manta birostris* revealed by archival tags and submersible observations. *Zoology*, in press.

Stewart, J.D., Jaine, F.R., Armstrong, A.J., Armstrong, A.O., Bennett, M.B., Burgess, K.B., Couturier, L.I., Croll, D.A., Cronin, M.R., Deakos, M.H. and Dudgeon, C.L., 2018. Research priorities to support effective manta and devil ray conservation. *Frontiers in Marine Science*, 5, p.314.

Stobart, B., Díaz, D., Álvarez, F., Alonso, C., Mallol, S. and Goñi, R., 2015. Performance of baited underwater video: does it underestimate abundance at high population densities?. *PLoS One*, 10(5), p.e0127559.

Stobart, B., García-Charton, J.A., Espejo, C., Rochel, E., Goñi, R., Reñones, O., Herrero, A., Crech'riou, R., Polti, S., Marcos, C. and Planes, S., 2007. A baited underwater video technique to assess shallow-water Mediterranean fish assemblages: Methodological evaluation. *Journal of Experimental Marine Biology and Ecology*, 345(2), pp.158-174.

Strayer, D., Glitzenstein, J.S., Jones, C.G., Kolasa, J., Likens, G.E., McDonnell, M.J., Parker, G.G. and Pickett, S.T., 1986. Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. *Occasional publication of the Institute of Ecosystem Studies*, 2(9).

Strike, E.M., Harris, J.L., Ballard, K.L., Hawkins, J.P., Crockett, J. and Stevens, G.M., 2022. Sublethal injuries and physical abnormalities in Maldives manta rays, *Mobula alfredi* and *M. birostris*. *Frontiers in Marine Science*, p.270.

Strutton, P.G., Coles, V.J., Hood, R.R., Matear, R.J., McPhaden, M.J. and Phillips, H.E., 2015. Biogeochemical variability in the central equatorial Indian Ocean during the monsoon transition. *Biogeosciences*, 12(8), pp.2367-2382.

Thorrold, S.R., Afonso, P., Fontes, J., Braun, C.D., Santos, R.S., Skomal, G.B. and Berumen, M.L., 2014. Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nature communications*, 5(1), pp.1-7.

Thums, M., Meekan, M., Stevens, J., Wilson, S. and Polovina, J., 2013. Evidence for behavioural thermoregulation by the world's largest fish. *Journal of the Royal Society Interface*, 10(78), p.20120477.

Triki, Z., Wismer, S., Levorato, E. and Bshary, R., 2018. A decrease in the abundance and strategic sophistication of cleaner fish after environmental perturbations. *Global Change Biology*, 24(1), pp.481-489.

Venables, S., McGregor, F., Brain, L., and van Keulen, M., (2016a). Manta ray tourism management, precautionary strategies for a growing industry: a case study from the Ningaloo Marine Park, Western Australia. *Pacific Conservation Biology*, 22(4), pp.295-300.

Venables, S., Winstanley, G., Bowles, L. and Marshall, A.D., (2016b). A giant opportunity: the economic impact of manta rays on the Mozambican tourism industry—an incentive for increased management and protection. *Tourism in marine environments*, 12(1), pp.51-68.



UNESCO (United Nations Educational Scientific and Cultural Organization). 2005. The Precautionary Principle World Commission on the Ethics of Scientific Knowledge and Technology (COMEST).

Ward-Paige, C.A., Mora, C., Lotze, H.K., Pattengill-Semmens, C., McClenachan, L., Arias-Castro, E. and Myers, R.A., 2010. Large-scale absence of sharks on reefs in the greater-Caribbean: a footprint of human pressures. *PloS one*, 5(8), p.e11968.

Watson, S.A., Allan, B.J., McQueen, D.E., Nicol, S., Parsons, D.M., Pether, S.M., Pope, S., Setiawan, A.N., Smith, N., Wilson, C. and Munday, P.L., 2018. Ocean warming has a greater effect than acidification on the early life history development and swimming performance of a large circumglobal pelagic fish. *Global Change Biology*, 24(9), pp.4368-4385.

Webster, C.N., Varpe, Ø., Falk-Petersen, S., Berge, J., Stübner, E., Brierley, A.S., 2015. Moonlit swimming: vertical distributions of macrozooplankton and nekton during the polar night. *Polar Biology* 38, 75–85.

Wheeler, C.R., Gervais, C.R., Johnson, M.S., Vance, S., Rosa, R., Mandelman, J.W. and Rummer, J.L., 2020. Anthropogenic stressors influence reproduction and development in elasmobranch fishes. *Reviews in Fish Biology and Fisheries*, 30(2), pp.373-386.

White, W.T., Corrigan, S., Yang, L.E.I., Henderson, A.C., Bazinet, A.L., Swofford, D.L. and Naylor, G.J., 2018. Phylogeny of the manta and devilrays (Chondrichthyes: Mobulidae), with an updated taxonomic arrangement for the family. *Zoological Journal of the Linnean Society*, 182(1), pp.50-75.

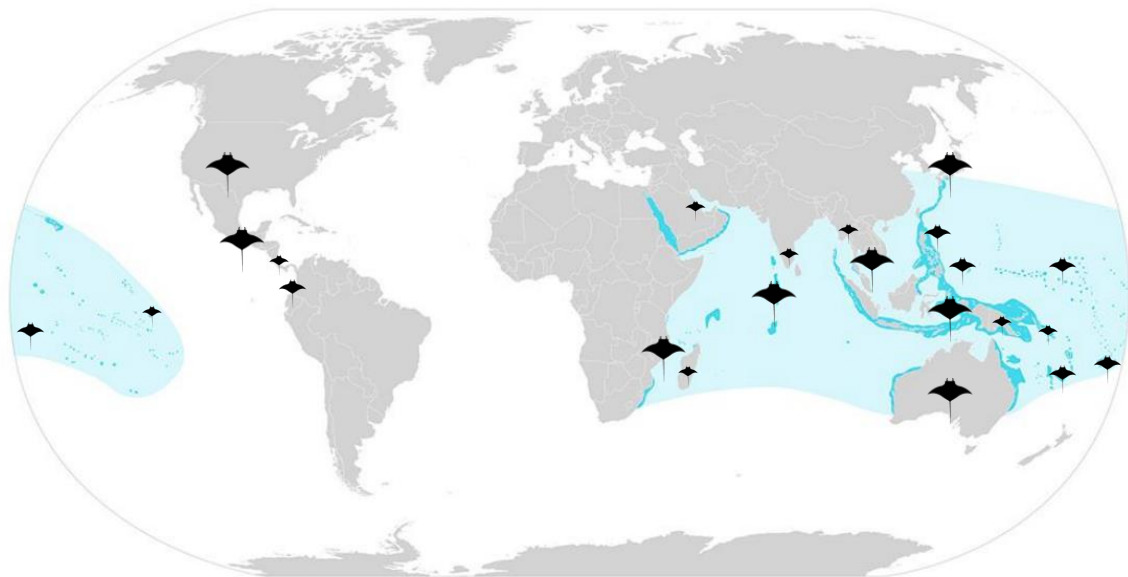
White, W.T., Giles, J., Potter, I.C., Dharmadi & Potter, I.C., 2006. Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. *Fisheries Research*, 82(1-3), pp.65–73.

Whitmarsh, S.K., Huveneers, C. and Fairweather, P.G., 2018. What are we missing? Advantages of more than one viewpoint to estimate fish assemblages using baited video. *Royal Society open science*, 5(5), p.171993.

Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, B., Froyd, C.A. & Myers, N., 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, 362(1478), pp.175–186.

## Supplementary Information

### Supplementary Figures



◆ : DEI of >US\$10m      ◆ : DEI of US\$1m-US\$10m      ◆ : DEI of <US\$1m

*Figure S1 – Distribution of reef manta ray (Mobula alfredi) throughout the Indo-Pacific region. Dark green = confirmed distribution, Light green = expected range. Including the direct economic impact (DEI) of manta ray tourism. DEI consists of estimate tourist expenditures on manta ray dives and associated spending. Reproduced from O'Malley et al., 2013; Stevens, 2016.*

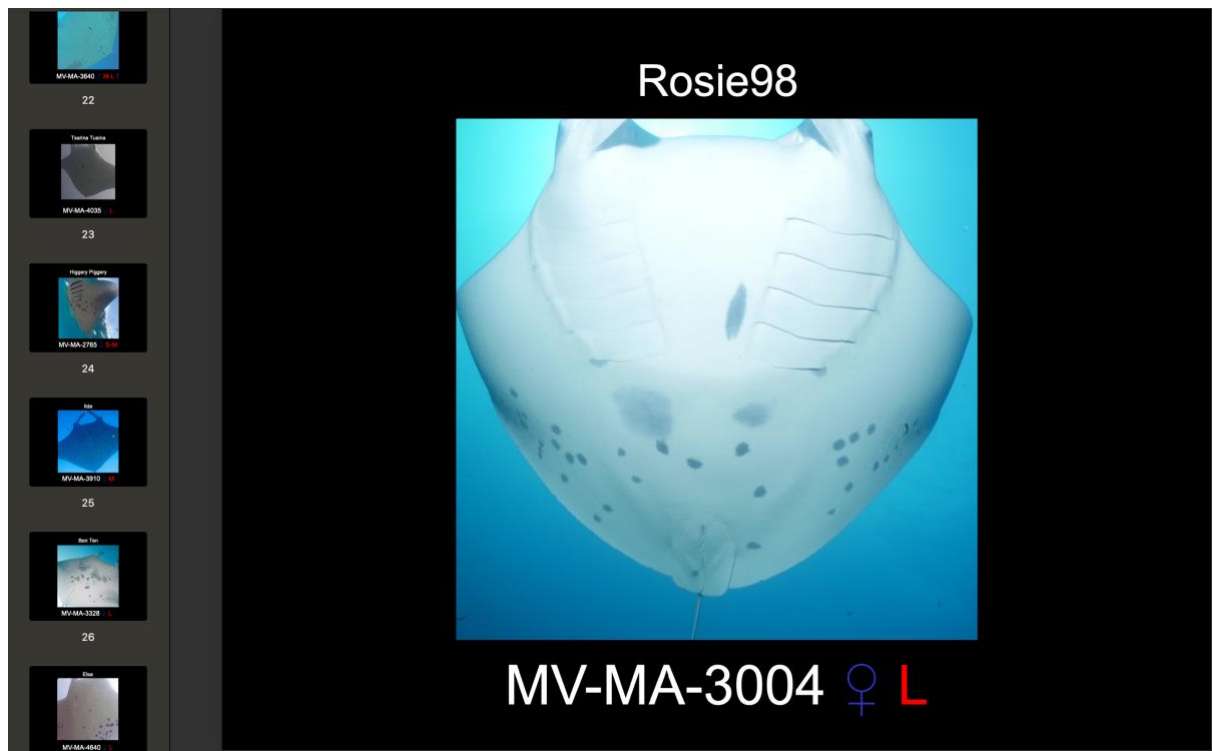


Figure S2 – The ‘Laamu Atoll – Branchial Identification Gallery’, featuring photo of the manta ray’s ventral side, name, identification code and sex. Additional information can include - Tail length: **S,M,L** (Short, Medium, Long); Tail Damage: **T**; Pectoral Fin Damage: **RP** or **LP** (right of left); Cephalic Fin Damage: **RC** or **LC** (right or left); Gill Damage: **RG** or **LG** (right or left).

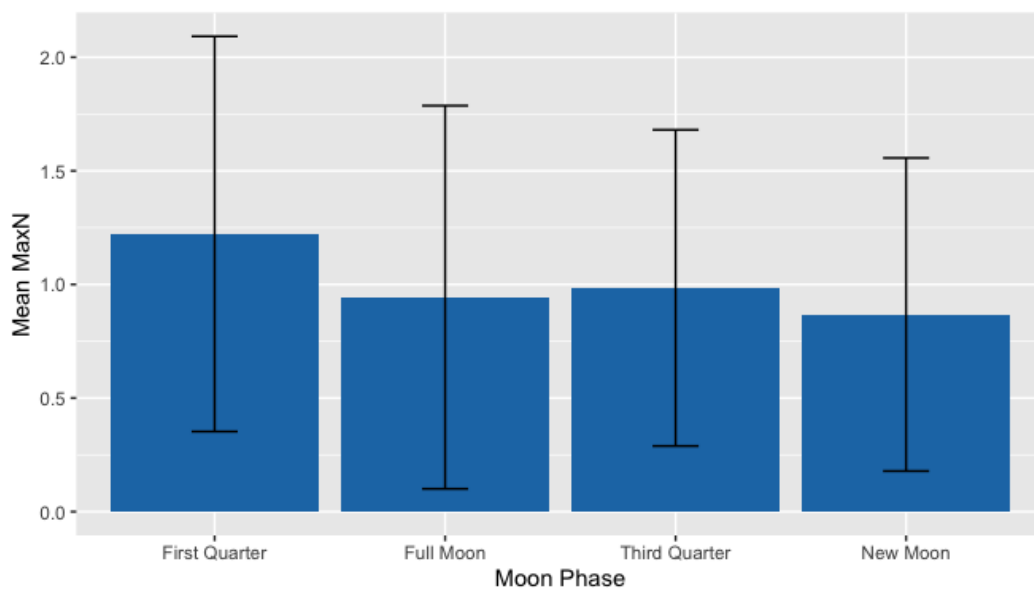


Figure S3 – The Mean MaxN of observed *M. alfredi* throughout the year for each moon phase.

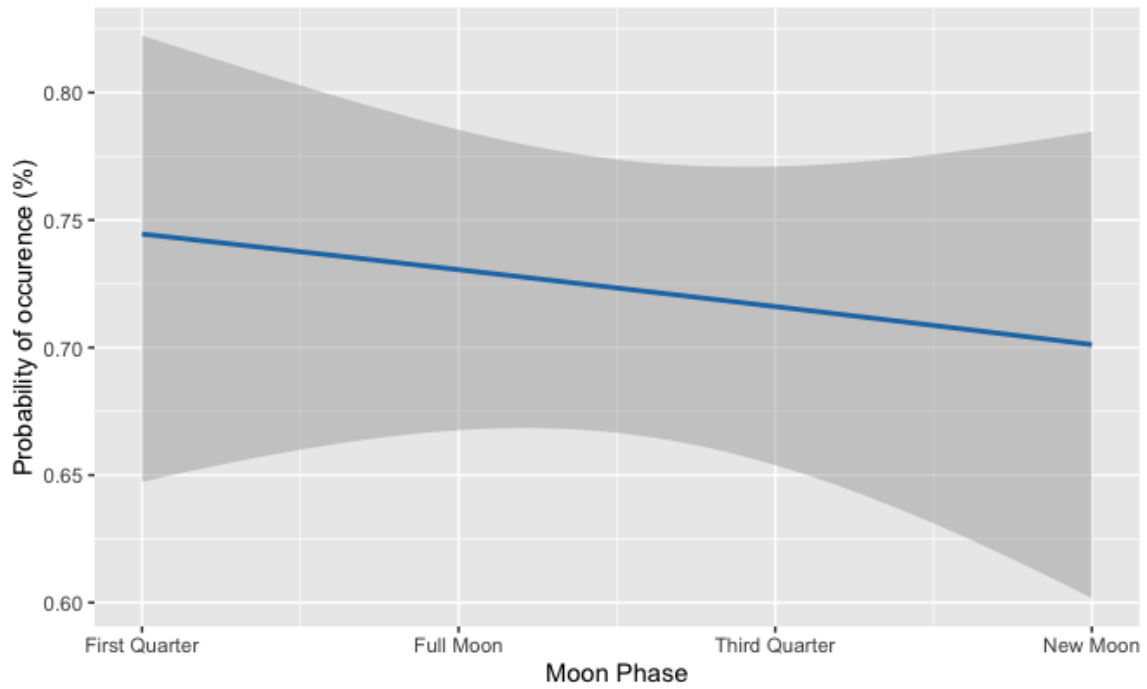


Figure S4 - The probability of *M.alfredi* occurrence at Shallow Block, Hithadhoo Corner over different moon phases. Shaded area details standard error.

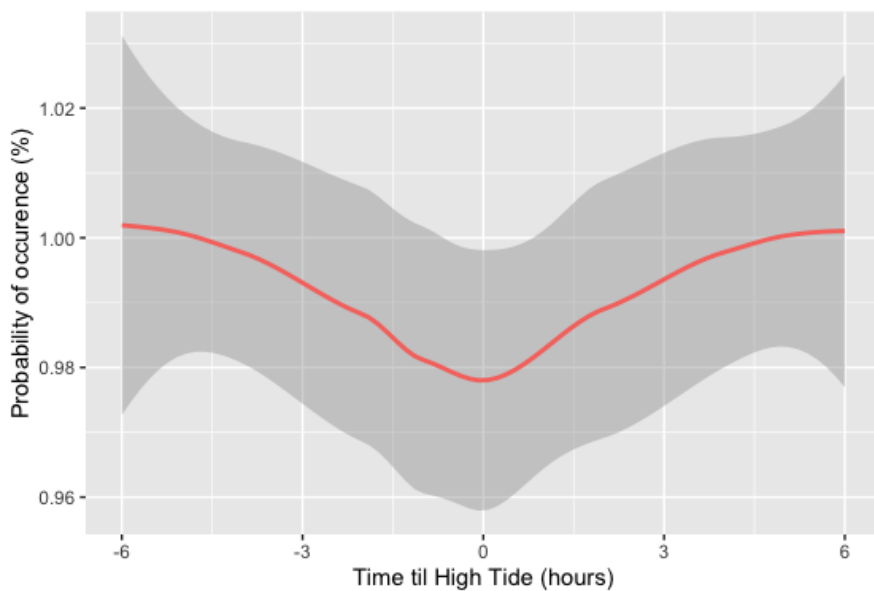


Figure S5 - The probability of *M.alfredi* occurrence at Shallow Block, Hithadhoo Corner over different tide states.

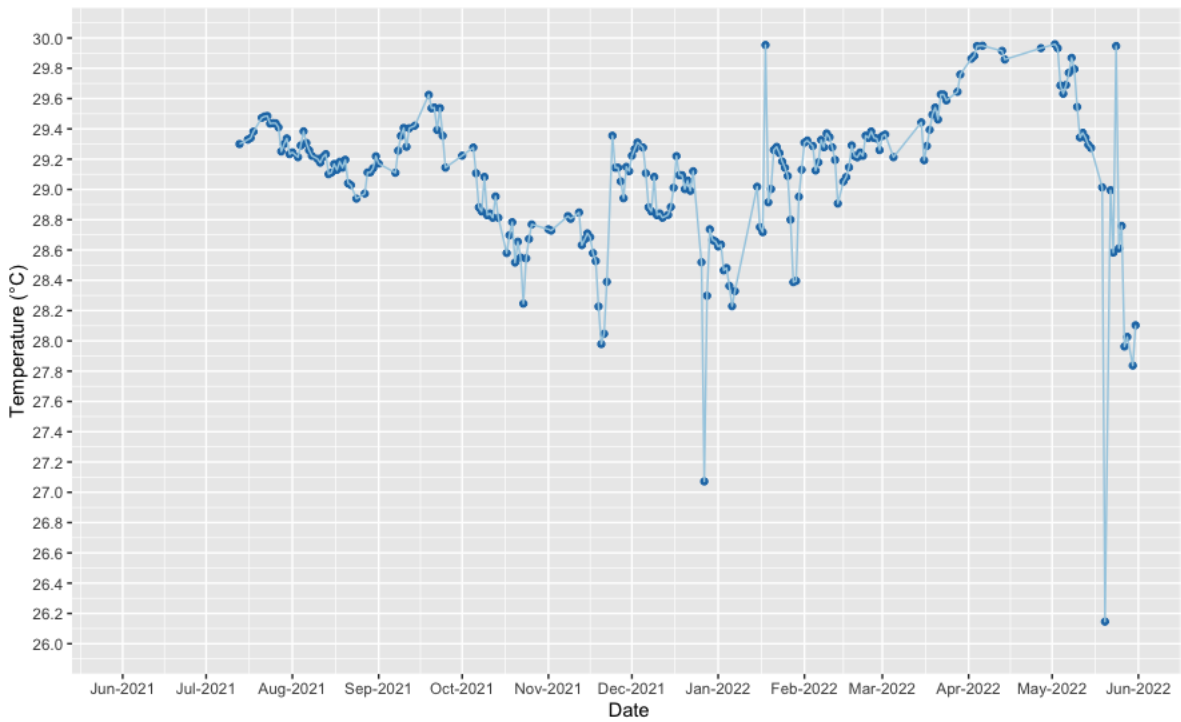


Figure S6 - The temperature at Shallow Block, Hithadhoo Corner, for each day recorded over the survey year.

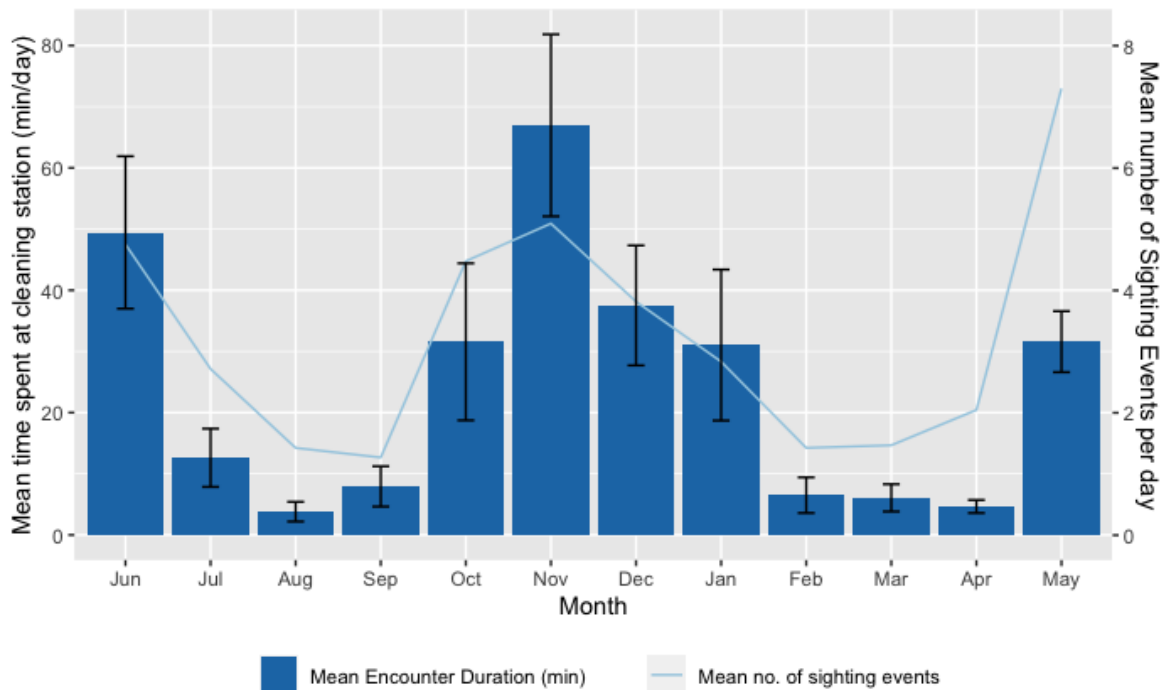


Figure S7 - Mean time *M.alfredi* spent at Shallow Block, and mean number of sighting events of each month over the survey year. Error bars display the standard error of mean time spent at the cleaning station.

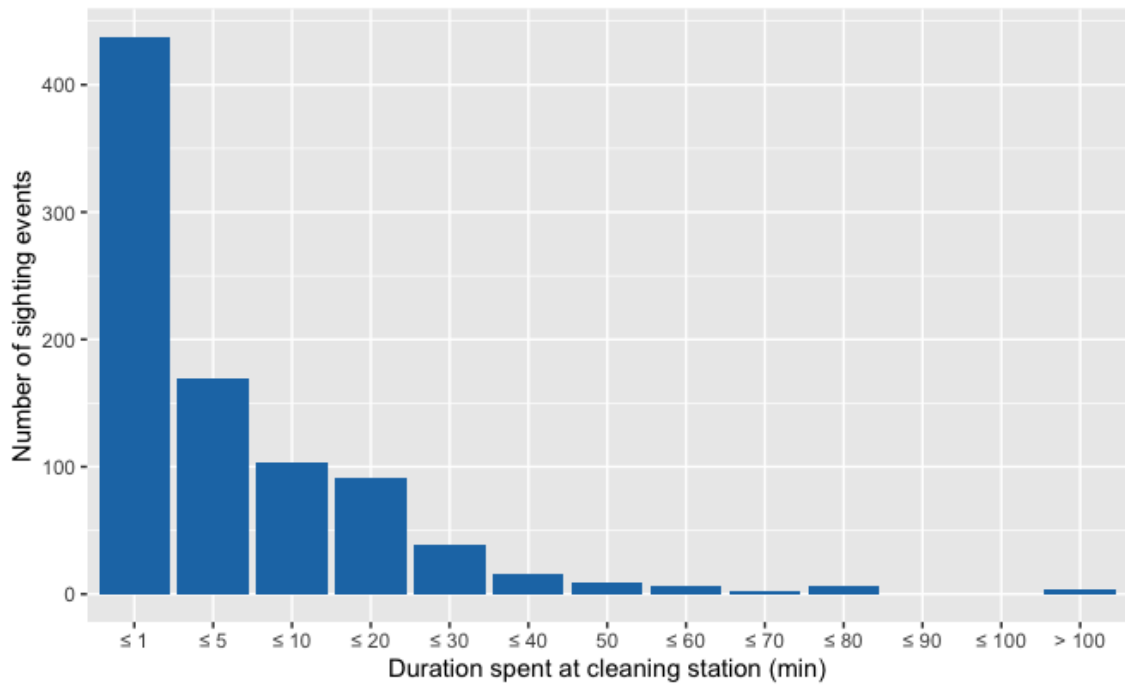


Figure S8 - The number of sighting events of different durations spent by manta rays at the cleaning station.

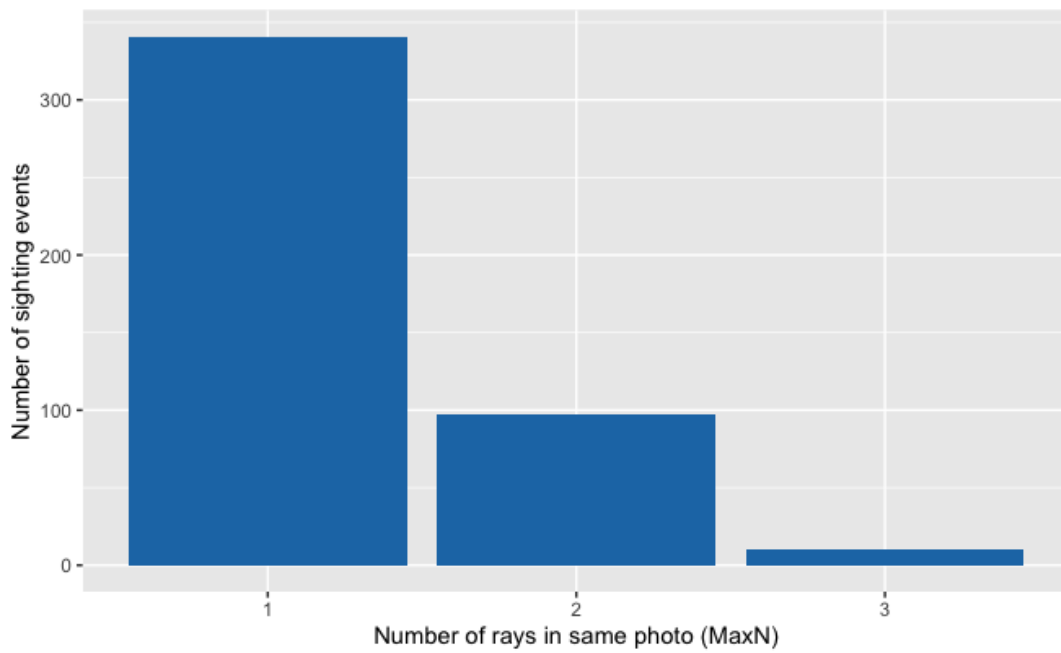


Figure S9 - The number of sighting events of different MaxN values of manta rays seen in photos.

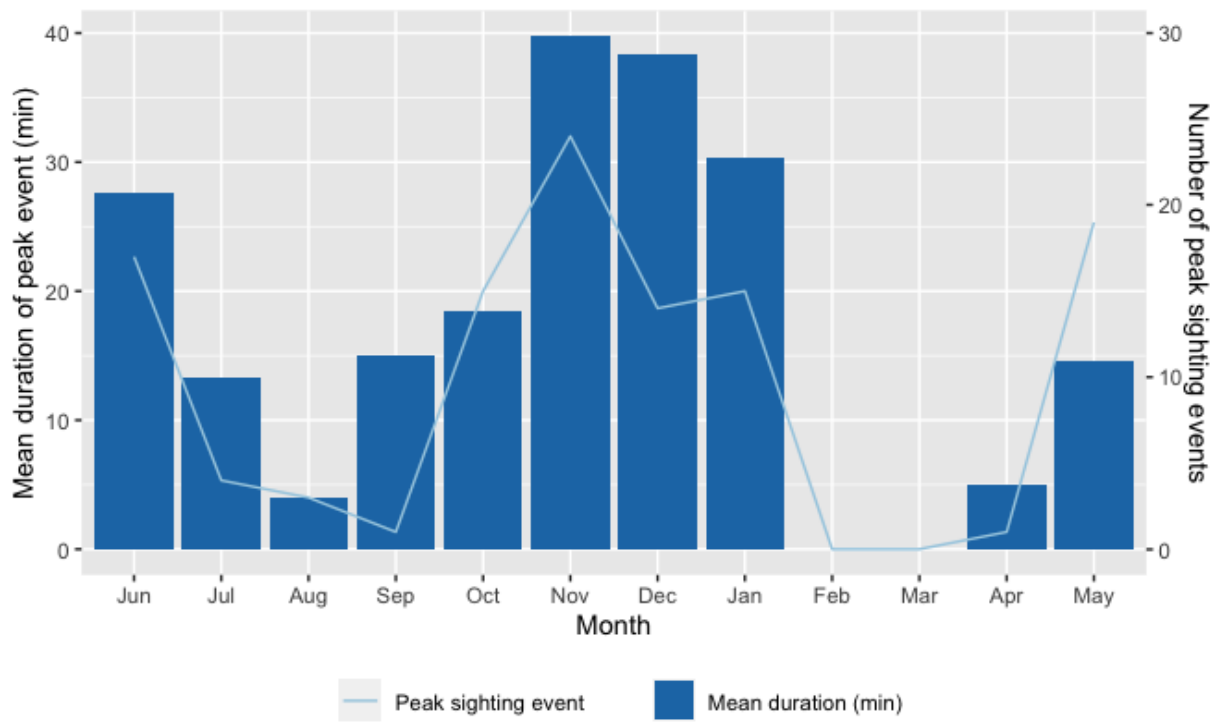


Figure S10 – The number of and mean duration of a peak sighting events over each month.





Figure S11 - Estimated number of manta rays per time interval over the sum of months.

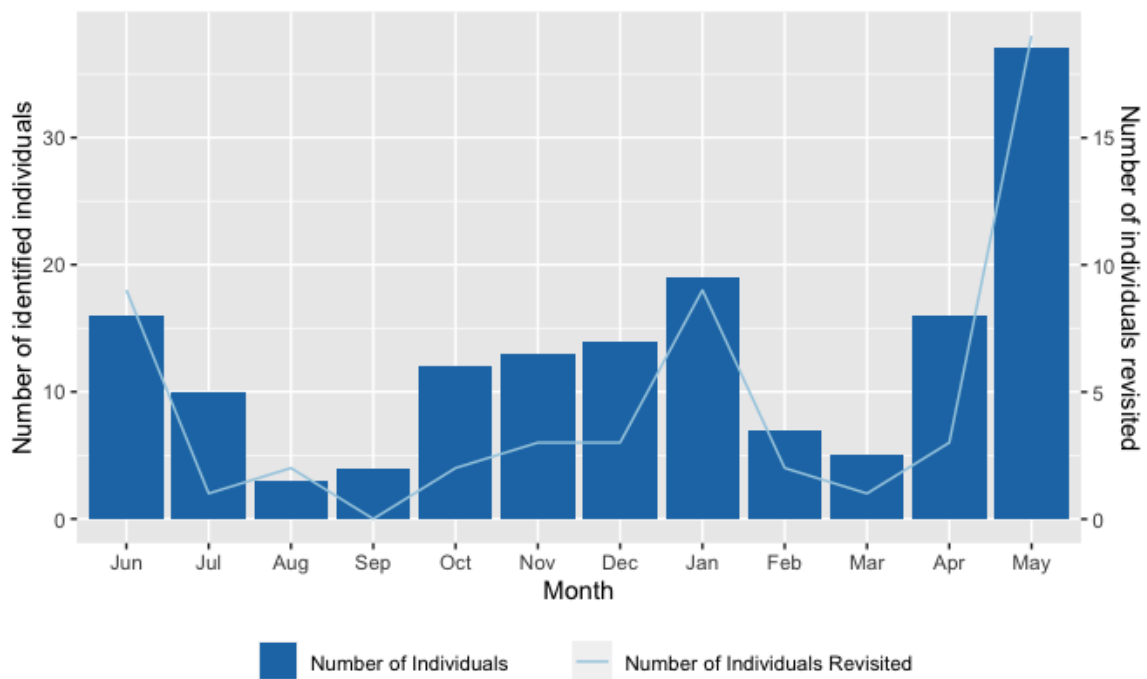


Figure S12– The number of identified individuals over each month and number of manta rays that revisited each month.

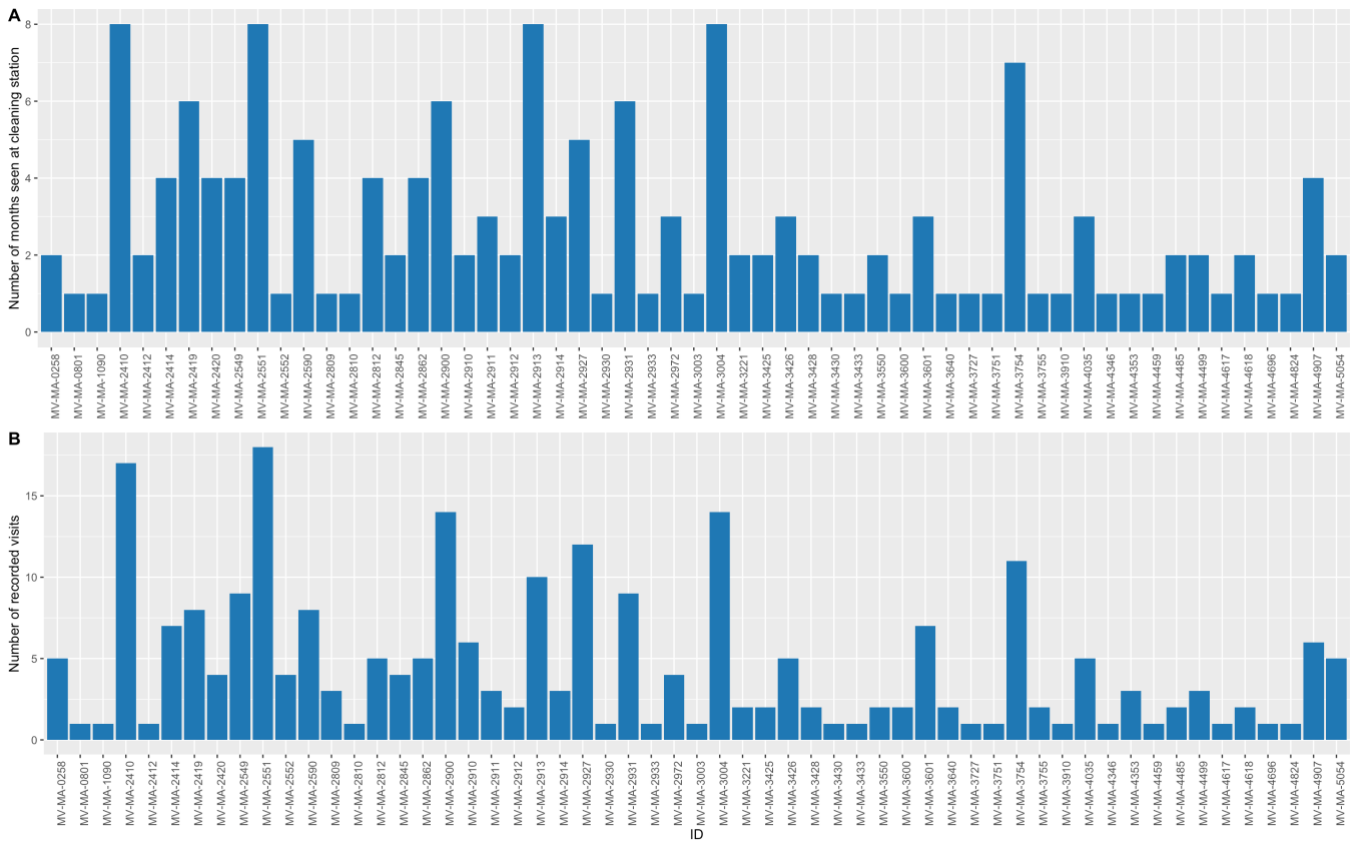


Figure S13 - (A) The number of months each identified individual was seen at the cleaning station for; (B) The frequency of visits of identified individuals over the year.

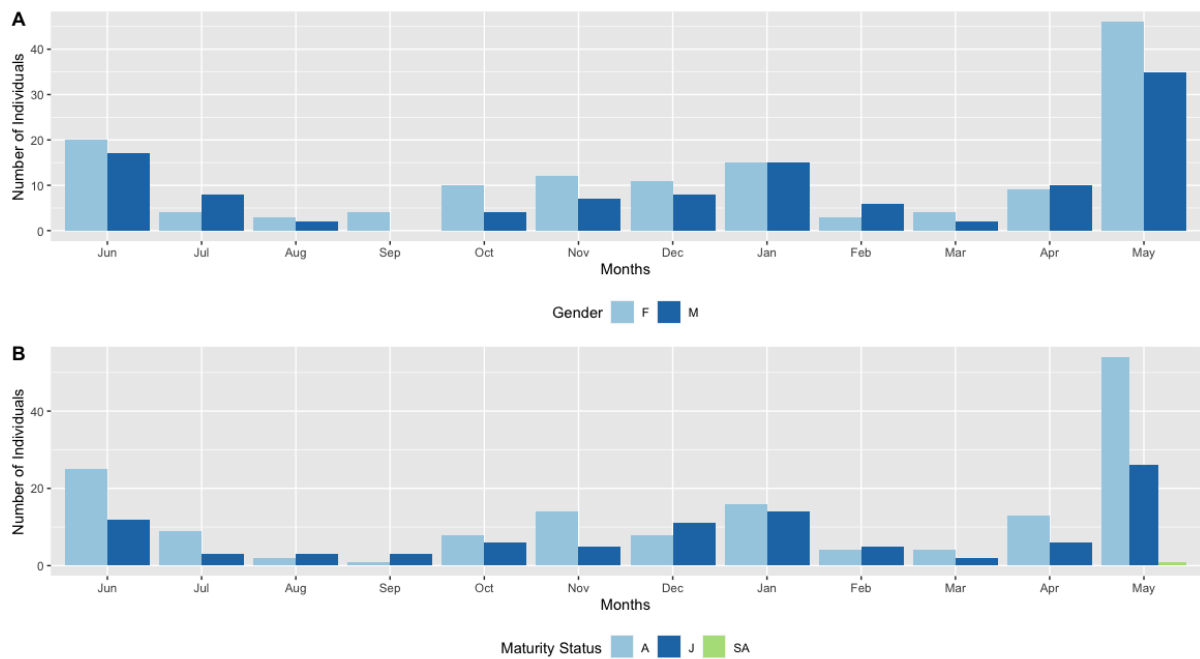


Figure S14 – Sex and Maturity Status: (A) The sex recorded within manta ray sightings, over months, F = Female, M = Male; (B) The maturity stage recorded within manta ray sightings over months, A = Adult, J = Juvenile, SA = Subadult.

## Supplementary Tables

Table S1 – Summary of all model output from the full model investigating the effect of the investigative factors on MaxN. MaxN ~ Moon + Temp + mean\_encounter + tide

	Df	Deviance	AIC	LRT	Pr(>Chi)
<none>		26.327	409.80		
Moon	3	27.536	405.01	1.2083	0.75101
Temp	1	27.684	409.16	1.3569	0.24407
Mean_encounter	1	31.181	412.66	4.8536	0.02759
Tide	1	26.532	408.01	0.2046	0.65101

Table S2 – Summary of all model output from the minimum adequate model (best fit) investigating the effect of the investigative factors on MaxN. MaxN ~ Temp + mean\_encounter

	Df	Deviance	AIC	LRT	Pr(>Chi)
<none>		159.67	545.76		
Temp	1	165.22	543.31	3.810	0.0404
Mean_encounter	1	186.75	564.84	25.342	4.802e-07

Table S3 – Summary of all model output from the human presence model investigating the effect of this factor on MaxN. MaxN ~ Total\_Human

	Df	Deviance	AIC	LRT	Pr(>Chi)
<none>		210.01	645.84		
Total_Human	1	210.09	643.92	0.08402	0.7719

Table S4 – Summary of all model output from the full model investigating the effect of the investigative factors on manta ray presence. Sighted\_nu ~ Temp + Moon\_Score + Tide

	Df	Deviance	AIC	LRT	Pr(>Chi)
<none>		11.819			
Temp	1	11.969	17.968	0.14980	0.6987
Moon_Score	1	12.059	18.059	0.24046	0.6239
Tide	1	11.821	17.821	0.00243	0.9607

Table S5 – Summary of all model output from the minimum adequate model (best fit) investigating the effect of the investigative factors on manta ray presence. Sighted\_nu ~ Temp

	Df	Deviance	AIC	LRT	Pr(>Chi)
<none>		290.80	294.80		
Temp	1	295.61	297.61	4.81303	0.02829

Table S6 – Summary of One-way Anova investigating the effect of human presence on mean encounter time.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
human	1	19.5	19.50	0.0422	0.8413
Residuals	10	4617.9	461.79		

Table S7 – Summary of One-way Anova investigating the effect of the number of days recorded on MaxN

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Human	1	1.3456	1.34560	2.5288	0.1429
Residuals	10	5.3211	0.53211		