Cleaning to Conservation: Remote Underwater Photographs Reveal Environmental Drivers and Resighting Patterns of *Mobula alfredi* in Laamu Atoll, Maldives.

MSc Research Project in collaboration with the Manta Trust.

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Words: 7991

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Target Journal:

Frontiers in Marine Science

Reasoning:

Frontiers in Marine Science is a well-established peer-reviewed scientific journal and is the third most-cited for the marine sciences. The underpinning themes and long-term messages echoed throughout the journal's publications run parallel to this study. They highlight that the development of knowledge marine spatial planners use to implement protective measures, is particularly poor. Also, Frontiers in Marine Science maintains all its publications as open access, allowing for a ubiquitous audience. This is especially key for developing countries, such as the Republic of Maldives, where funding opportunities are suppressed and may not allow for journal subscriptions.

Abstract

Reef manta rays (*Mobula alfredi*) are threatened by anthropogenic exploitation. Fishing and tourism coupled with conservative life history traits, like late maturation and low fecundity, have made this species vulnerable to extinction. Site-specific spatiotemporal ecological knowledge at key aggregations is imperative for effective marine protection. To understand drivers of abundance around cleaning stations and residency patterns of reef manta rays, passive remote underwater photosystems were deployed at four known cleaning sites around Laamu, a remote Maldivian atoll. Between March 2021 and May 2023, 455,458 photos were analysed for reef manta ray presence and identification. Generalised linear models revealed significant effects of monsoon season, chlorophyll-a concentration, moon state, and time of day on abundance, while human presence had no effect. Branchial spot patterns were assessed for 629 photos, allowing for 81 unique individual identifications, over 50% of all identified in the atoll. Our results suggest that Laamu has a small, annual, resident reef manta ray population, which significantly increases in response to high chlorophyll-a concentrations, low illumination moon states, season, and time of day. Broadly, seasonal productivity increases cleaning station abundance, suggesting Laamu has productive foraging patches in proximity. This understanding can guide marine spatial planners on the effective implementation of Laamu's first marine protected area management plan. It also raises questions of the true interconnectedness of Laamu with other atolls and highlights clear knowledge gaps. Additionally, such findings build on cleaning site suitability understanding, and at what conditions they are favourable. Effective, enforced, and informed protection will aid in reducing future climate, tourism, and fishing pressures, all threatening reef manta rays.

1. Introduction

The world's ocean provides a diversity of life support systems but has faced an increasing amount of pressure from anthropogenic exploitation since the Industrial Revolution (Link & Watson 2019; Venegas *et al.* 2023). Current marine protection is inadequate to protect species and their habitats (Gill *et al.* 2017). The awareness of the need for specific ecosystem-based knowledge has grown with insights from observational data and remote monitoring used to improve marine protection (Stewart *et al.* 2018; Grorud-Colvert *et al.* 2021). Declines in pelagic and inshore elasmobranch populations have increasingly been highlighted following a rise in attention (MacNeil *et al.* 2020; Jorgensen *et al.* 2022). As per the International Union for Conservation of Nature (IUCN), 32% of elasmobranchs are listed as threatened with extinction and a further 37.5% deficient in data to make an assessment (Jorgensen *et al.* 2022). Reef manta rays (*Mobula alfredi*; hereafter: manta/s) are found circumglobally in tropical and subtropical waters (Couturier *et al.* 2012). These conspicuous and charismatic animals are bound to a life of perpetual motion, and spend much of their time in depths less than 50m, searching for productive foraging patches to sustain their large mass (Couturier *et al.* 2012; Stewart *et al.* 2018; Peel *et al.* 2020). Manta trade, globally, is regulated by the Convention on International Trade in Endangered Species (CITES) appendix II, Conservation of Migratory Species (CMS) appendix I and II, and locally within 16 nations, including the Republic of Maldives (hereafter: Maldives; Croll *et al.* 2016). Recent studies call for these lawful protective measures to be accompanied by regional-specific, holistic management (Graham *et al.* 2012; Stevens 2016; Andrzejaczek *et al.* 2020).

Marine protected areas (MPA/s) form the basis of spatial protection but vary in success (Gill *et al.* 2017; Grorud-Colvert *et al.* 2021). Without enforced, effective management plans, MPAs provide little benefit and fall into the 'paper park' paradigm, a ubiquitous issue apparent in ~70% of MPAs globally (Edgar *et al.* 2014; Gill *et al.* 2017; Roberts *et al.* 2018; Bohorquez *et al.* 2022). There are anecdotal cases of successful manta management. A network of nine MPAs, designated in 2007, have

seen a substantial increase in the manta population within Raja Ampat (Setyawan *et al.* 2022). However, limited understanding, extensive migrations, fragmented sub-populations, and notable absence of commercial interest have led mantas to be understudied and under-protected (Dewar *et al.* 2008; Saltzman & White 2022). The necessity for large, highly protected, managed and community-driven MPAs is clear (Grorud-Colvert *et al.* 2021). Manta aggregations, such as cleaning stations, can provide substantial benefits via relatively small, informed areas of protection (Palacios *et al.* 2023). While regions like the British Indian Ocean Territory (BIOT) can feasibly protect the entire local manta populations' home ranges (Andrzejaczek *et al.* 2020), often, this is not socioeconomically or behaviourally feasible (Palacios *et al.* 2023). Therefore, a baseline of ecological knowledge of a site's use must be developed to enable marine spatial planners to effectively allocate limited resources for manta conservation across their entire range.

Cleaning forms key aspects of many large reef vertebrates' life histories, whereby mutualistic interactions with *Labroides sp.* aid the ridding of parasites, dead skin, and mucus (Grutter 1996; Hay *et al.* 2004; O'Shea *et al.* 2010). Aggregations, smaller than those associated with foraging, occur around cleaning stations for intra-specific interactions like courtship and lekking (Jaine *et al.* 2012; Stevens 2016; Harris & Stevens 2021). Conversely to foraging areas, which can occur offshore or within inter-atoll lagoons, cleaning stations are confined to shallow reefs and therefore of easier, predictable exploitation (Armstrong *et al.* 2019). Mantas are considered extreme *K*-selected species, with gestations over a year, long post-partum recoveries and single pup pregnancies (Graham *et al.* 2012; Stevens 2016). These reproductive characteristics coupled with diurnal migrations, and aggregatory behaviours render the chance of over-exploitation high. Manta populations worldwide are, per the IUCN, vulnerable to extinction and have fallen victim to a plethora of anthropogenic pressures (Dulvy *et al.* 2014; Marshall *et al.* 2022). These include intentional capture for gill rakers, unintentional by-catch in active and ghost nets, boat strike, habitat degradation, climate change-related effects and un-monitored tourism (Stevens & Froman 2018; Murray *et al.* 2020). For example,

Baa Atoll, Maldives welcomes more than 25,000 tourists annually which have been shown to affect manta behaviours in 37% of encounters (Murray *et al.* 2020) implied to cumulatively impact fitness (Venables *et al.* 2016). Recent declines in manta populations are threatening their ecological and economic importance (Heithaus *et al.* 2008; McCauley *et al.* 2015; Stewart *et al.* 2018). Sub-populations generally coincide with less developed nations and so the ~US$140 million predicted revenue in 2013 from global tourism (O'Malley *et al.* 2013), creates high levels of socioeconomic dependence on this species. The intrinsic vulnerability of mantas and evident exploitation requires adequate MPAs to conserve their ecological and socio-economic importance.

Globally, manta populations are fragmented and range in size from hundreds to thousands, with population connectedness non-linear (Deakos *et al.* 2011; Kashiwagi *et al.* 2011; Couturier *et al.* 2012). Geographical barriers such as deep channels and cold water serve as key isolators of population dispersal, as well as high productivity and quality cleaning stations fuelling site fidelity (Espinoza *et al.* 2016; Peel *et al.* 2019b). The presence of mantas at specific sites, such as cleaning stations, varies geographically (Armstrong *et al.* 2016; 2021). Opportunistic self-contained underwater breathing apparatus (SCUBA) and fisher observations have been used historically to develop region-specific baselines of knowledge (Anderson *et al.* 2011a; Stevens 2016). Although these methodologies are useful, considerable limitations, such as the evident effect of human presence on behaviour, temporal restrictions and high effort make them inadequate for quick and unbiased assessments of manta populations, essential in consideration of the variety of threats they face. Remote underwater photo (RUP) systems have proven effective for manta population assessments and long-term, unbiased and continuous monitoring of cleaning sites before (Peel *et al.* 2019b). Applying a combination of methodologies to assess manta populations is key for the identification of refuges, quantifying the importance of specific sites, and priorities for protection. It is therefore vital for countries with high manta abundances, burgeoning threats, and remote regions, such as the

Maldives, to improve knowledge of their local manta population for the implementation of specific MPAs and deploy advanced study methodologies.

Merely 0.5% of the Maldivian exclusive economic zone (EEZ) is protected by 42 MPAs (Stevens & Froman 2018). Only one has an active management plan, delineating MPAs within the Maldives as little more than paper parks (Mohamed 2007; Rife *et al.* 2013; Stevens & Froman 2018). Mantas are nationally protected, and the Maldives is thought to have the world's largest known sub-population (Stevens 2016). Between 2006 and 2008, direct tourism from mantas was estimated at ~US$8.1 million annually, a figure likely far larger considering the growth of visitors over the last decade (Anderson *et al.* 2011b; Stevens & Froman 2018). Although direct capture of mantas is illegal in the Maldives (Maldives EPA 2014), the EEZ is surrounded by fishers, some from Sri Lanka illegally fishing within it (Fernando & Stewart 2021). Habitat degradation, boat strike and unmanaged tourism further threaten this sub-population (Stevens 2016; Harris *et al.* 2020; Strike *et al.* 2022). Except Hanifaru Bay (Armstrong *et al.* 2021), few important aggregation sites have been intensively studied. Maldives-wide findings have detailed the general importance of the nation, but many have shown little regard for the remote southern atolls; Huvadhu, Fuvahmulah, Addu and Laamu (Anderson *et al.* 2011a; Stevens 2016; Harris *et al.* 2020). Adequate protection relies heavily on detailed understandings of local populations, how they utilise their environments and influencers of distribution (Jaine *et al.* 2014; Barr & Abelson 2019). Specific knowledge on mantas has already directly driven the establishment of two MPAs in the Maldives; Hanifaru Bay and Anga Faru (Manta Trust 2022). Without comprehensive and site-specific studies, the development of effective management plans risk becoming ad-hoc and insufficient.

This study aimed to build a comprehensive assessment of the Laamu atoll manta population and their cleaning stations. To develop a spatiotemporal understanding and feed directly into the foundations of future MPA management plans, these questions were explored via passive RUP systems:

1) Which environmental variables are driving seasonal and diurnal presence?

2) What can re-sightings of individual mantas tell us about their residency patterns and movement behaviour?

2. Methodology

2.1 Study Site

The Maldives consists of 26 administrative atolls, located in the central Indian Ocean (Fig.1). Monsoon seasons drive productive upwellings bi-annually in Laamu (Harris *et al.* 2020). Laamu consists of 82 islands, fringing coral reefs and characterised by six channels that drop steeply to abyssal depths (Fig.1; Sluka 2000). RUP systems were deployed at four known manta cleaning sites; Hithadhoo Corner, Fushi Kandu, Boduhuraa Beyru and Fonadhoo Beyru (Fig.1;Table 1). All were identified as per Potts's (1973) criteria; observing multiple manta cleaning events and territorial residency of adult cleaner wrasse (*Labroides sp.*).
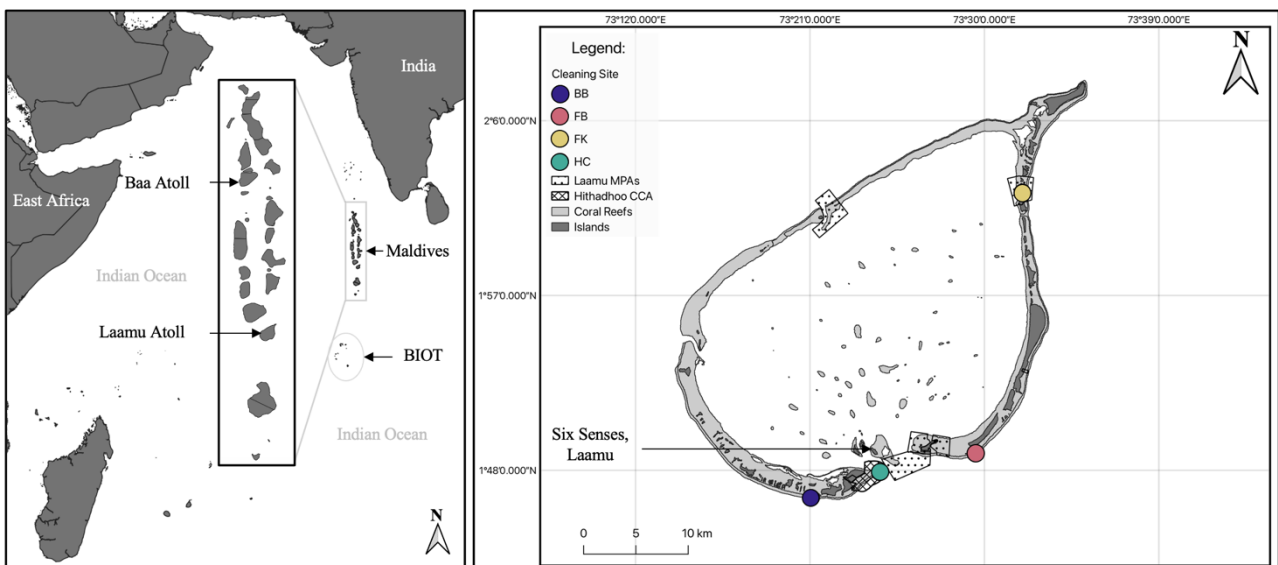

Figure 1 – **A)** Location of the Republic of Maldives in the Indian Ocean and enlargement of the 26 administrative atolls. BIOT: British Indian Ocean Territory. **B)** Map of Laamu atoll with the four RUP deployment locations; Boduhuraa Beyru (BB; Purple), Fonadhoo Beyru (FB; Red), Fushi Kandu (FK; Yellow) and Hithadhoo Corner (HC; Green). Polygons detailing designated marine protected areas (MPA) and Hithadhoo Baaneykolhu Community Conservation Area (CCA), recently proposed by Hithadhoo Council.

Table 1 – Summary of survey sites. * denotes an estimated value. All distances were measured from Six Senses Resort, Laamu.

Name	Other Name	Co-ordinates	Period Observed	Location Type	Depth (m)	Size (m)	Distance (km)
Hithadhoo Corner	Kandu Kolhu	1°47'53.76"N 73°24'35.99"E	26/01/2020 - 18/05/2023	Channel	Shallow: 14.5 – 17.7m Yellow: 18.3 – 22.2m	Shallow: 24x12m* Yellow: 17x18m	2.5
Fonadhoo Beyru	N/A	1°48'52.21"N 73°29'32.03"E	13/09/2022 - 20/03/2023	Outer-reef Slope	24.9 – 26.7m	5.5x6.5m	11
Fushi Kandu	N/A	2° 2'19.12"N 73°31'57.29"E	08/05/2022 - 21/04/2023	Channel	11.4 – 15.3m	13x8m*	30
Boduhuraa Beyru	Kurethi; Deep and New	1°46'35.57"N 73°21'4.78"E	05/01/2022 - 13/05/2023	Outer-reef Slope	Deep: 26 – 28m* New: 23 – 25m*	Deep: 10x10m* New: 8x5m*	14.5

2.2 RUP Deployment

All sites were accessed from Six Senses Laamu Resort, Olhuveli Island (Fig.1) via boat using SCUBA. Hithadhoo Corner is at the western edge of the Gadhoo-Hithadhoo Channel (Fig.1) and consists of five distinct coral bommie cleaning station blocks, namely, Shallow, Ridge, Yellow, Split and Turtle (Supp.Fig.1). RUPs were primarily deployed on Shallow Block due to frequent observations of manta cleaning during the trial phase. Fushi Kandu is a single cleaning station channel site, with RUPs deployed since May 2022. Boduhuraa Beyru is an outer reef characterised by several cleaning stations, with two used for RUP deployments since January 2022 (Table 1). Fonadhoo Beyru is another outer reef with RUPs deployed on a single deep cleaning station from September 2022.

Three RUP systems were used; one, a single GoPro HERO® 4 (12 megapixels, mode: wide angle, memory: 128GB), two and three, single GoPro HERO® 8 Blacks (12 megapixels, mode: wide angle, memory: 128GB), all with ~160° fields of view (Parton *et al.* 2023). Cameras were connected to Voltaic Systems© batteries (19,200mAh) and timelapse settings configured to take a single-frame photo every minute during daylight hours. Deployments were typically scheduled between 05:59 and 17:59, although soak times varied. Cameras were secured in custom-built housings and placed onto cleaning stations during research-designated dives, with standardised orientations. Shallow Block, Hithadhoo Corner had a custom-made concrete block placed onto bare reef to attach the systems to.

A compass was used at Fushi Kandu, Boduhuraa Beyru and Fonadhoo Beyru stations. Supplementary straps and weights were used to secure the cameras onto dead or bare reef and optimise the camera's view. Rubble was used to camouflage the systems.

2.3 RUP Photo Analysis

The maximum number of individuals in the frame, maxN, was recorded for each photo which contained mantas or humans (SCUBA diving or snorkelling). Upon a sighting, an estimation of the total period either a manta or human used a specific site was summarised into sighting events. Sighting events were considered terminated if a manta or human had not been seen for ≥10 minutes since the previous sighting. Those of a single photo were classed as 1 minute in length. Encounter durations per sighting event were defined as the interval between the first photo to the last. Maximum maxN for a sighting event was used as proxy for the total number of mantas for that specific event.

Adequate photos of branchial spot patterns were identified, as per Kitchen-Wheeler (2010) and Stevens (2016) methodologies, and recorded as confirmed number of mantas. They were manually matched to the regional Laamu database, which contained 144 different branchial patterns, as of June 2023, or the national database which contains >5000. Disc size is a proxy for maturity (Stevens 2016), which could not be quantified via the RUP, so pre-known maturity status from the databases were used. Sex was identified via claspers, which are present for males and absent for females (Deakos *et al.* 2011; Stevens 2016). Both the confirmed and highest maxN measures of abundance formed guaranteed metrics. Daily estimated abundances were calculated as follows:

$$Daily\ Estimated\ Abundance\ =\ \Sigma\,sighting\ event\ maximum\ maxN$$

2.4 Environmental Variables

Environmental variables were measured to understand their influence on manta abundance. Water temperature was measured in-situ at Hithadhoo Corner and Fushi Kandu using HOBO Pro V2 loggers (±0.2°C) and TCM-x Current Meters (Lowell Instruments LLC; ±0.1°C). HOBOs were placed adjacent to RUP deployment locations (Supp.Fig.1). Temperature was averaged for each survey day. TCM-x Current Meters use 3-axis accelerometers and magnetometers to obtain current speed (cm/s) and heading (360°). TCM-x Current Meters were set to record every minute and strategically placed to reduce physical current obstructions from the cleaning stations (Supp.Fig.1) between; December 2022 and March 2023. Speed and heading were averaged into hourly intervals and paired to those used for the daily variance (see section 2.5.2). Current data from Fushi Kandu could not be used due to drifting of the meter into the reef.

Large seasonal changes lack definite and consistent start and end times (Aslam & Kench 2017). Despite, seasonality was defined as described by Anderson *et al.*, (2011a); May to October the southwest (SW) monsoon, December to March the northeast (NE) and April and November as two months of retreat. Moon phases were extracted from an online database (https://www.timeanddate.com) and categorised into four states: new, first quarter, full, and third quarter and assigned to each survey day. Tidal charts were obtained from the Maldives Meteorological Service (https://www.meteorology.gov.mv) for Gan and used for all cleaning stations. Tide states were defined into four categories: high, ebb, low, and flood. High and low tides were rounded to the nearest hour and categorised into a three-hour period; the hour of and ±1 hour (O'Shea *et al.* 2010). Interval periods between low and high and high and low were defined as the flood and ebb, respectively. Both consisted of three hours but varied with tidal periods. Daily 0.25°x0.25° chlorophyll-a (mg/m^{-3}) data, from depths of ~0.4m, were obtained from Copernicus (https://www.copernicus.eu) through the Global Ocean Biogeochemistry Analysis and Forecast product (E.U. Copernicus Marine Service Information 2023) and assigned to each survey day. The

data were sourced from models, and tested to be highly correlated with satellite and BGC-Argo measurements (correlation coefficient: 0.81; RMSD: 0.59) and quality-approved in December 2022 (Lamouroux *et al.* 2022).

2.5 Statistical Analysis

2.5.1 Seasonal Variance

The estimated number of mantas, along with maxN and confirmed number, collectively provided the foundations of presence. To understand the linear relationship between the estimated and guaranteed number of mantas, confirmed and maxN, non-parametric Spearman's rank correlation tests were used. The outcomes of such provide insights into whether it was appropriate to continue with the estimated metric. Significant positive correlations support the effectiveness and inclusion of such metrics as response variables.

To understand the variation in manta abundance, two Generalised Linear Models (GLM) were used, with each survey day representing a data point. The rate of estimated manta presence per photo per day was calculated using the following formula:

$$Rate\ of\ Estimated\ Mantas = \frac{Estimated\ Number\ M.alfredi}{Total\ Survey\ Photos}$$

The rate was used as the response variable in the GLMs, which was modelled with a Gaussian error structuring and 'identity' link function. Model one analysed the predictors; monsoon season, cleaning site, moon state, and chlorophyll-a. Temperature was omitted from model one due to 315 days of missing data. Model two aimed to understand the influence of temperature by fitting the predictors; monsoon season, cleaning site, moon state, chlorophyll-a, and mean temperature. Both included an

interactive term between monsoon season and site, introduced to explore combined effects of these variables. Each model was fitted inclusive and exclusive of interactive terms. Model comparisons were conducted via ANOVA likelihood ratio tests, with a Chi^2 test function. Significant improvements to model fit resulted in interactions being retained. Model selection involved backward elimination of the least significant predictor (P>0.05), until the Minimum Adequate Model (MAM) remained. Estimated Marginal Means (EMM) Bonferroni pairwise post-hoc tests were conducted, via the 'emmeans' package to identify the significance of categorical variables (Lenth *et al.* 2023).

2.5.2 Diurnal Variance

Fine-scale daily variance of manta presence was explored by looking at each hour per survey day. Start times for sighting events were rounded to the nearest hour($\pm$). Sighting event maxN was used as the measure of abundance. For hours which recorded more than one sighting event, the sum maximum maxN was calculated. Two GLMs, with Gaussian distributions, as above, were used to understand how each predictor may influence sum maxN. Current data was only available for a short period, at Hithadhoo Corner, so necessitated a second model. Model one analysed; sum human maxN, cleaning site and hour (05:00–19:00). Model two analysed; sum human maxN, hour, and mean current speed and heading per hour. As above, MAMs were determined, and EMM used to identify the significance of each categorical variable. A third model was constructed to explore the influence more mantas had on sighting duration. A Gaussian GLM as above was used along with sighting duration (minutes) as the response and sum maxN as a predictor. These variables were also summarised into hour categories.

3. Results

3.1 Deployment Summary

A total of 133 RUP systems were deployed between March 2021 and May 2023. These consisted of 744 days of footage, totalling 455,458 photos, comprising 7,579 hours and 41 minutes. All sites experienced inconsistent survey efforts. Unbalanced effort favoured Hithadhoo Corner, consisting of 92 RUP deployments over 531 days and 71.32% (n=455,458) of total photos analysed. Comparatively, 20 deployments of 120 days, were soaked at Fushi Kandu with 76,354 photos analysed (16.7%; n=455,458). Bodhuraa Beyru and Fonadhoo Beyru were the least studied sites with 16 and 5 deployments over 61 days and 32 days, respectively. A total of 32,977 photos were analysed (7.24%; n=455,458) at Boduhuraa Beyru and 21,303 photos (4.67%; n = 455,458) at Fonadhoo Beyru. Similarly, surveys per month were also unequal across sites (Supp.Fig.2). The inter-site bommies used for camera deployments have varied at Hithadhoo Corner and Boduhuraa Beyru. At Hithadhoo Corner, prior to July 2021, cameras were deployed at Yellow (27 days), Split (8 days) and Turtle (8 days) Blocks. Since, all RUPs were positioned at Shallow. The identification of a new cleaning bommie at Boduhuraa Beyru, during 2023, saw two RUPs deployed for a total soak time of seven days.

As well as their use for identifying the presence of mantas, the RUPs identified: their ecological importance, such as defecating on cleaning sites, inferred social integrations and breaches of the Manta Trust's tested code of conduct (Supp.Fig.3; Murray *et al.* 2020). For example, in April 2023 nine divers were captured swimming over Shallow Block cleaning site, Hithadhoo Corner (Supp.Fig.3). The clarity of photos varied, due to biofouling, floating debris, and reef fish, which all caused frequent obstructions to view (Supp.Fig.3). Infrequent system interference, from humans, strong currents and swells, which resulted in orientation changes and obstructions, also compromised system view.

3.2 Seasonal Variance

Over the 744 survey days, a total of 2,599 mantas were estimated to have been sighted, with a mean ($\pm$SD) of 3.54$\pm$4.38 per day (range=0–22). Both the daily confirmed number of mantas and the maxN were significantly correlated with the daily estimated abundance and displayed strong monotonic positive correlations (Spearman's rho=0.659; $P<0.01$; Spearman's rho=0.864; $P<0.01$, respectively). Generally, a mean of 0.55$\pm$0.66% of photos had an estimated manta present (range=0%–3.05%; n photos=455,458). Of these, 240 days had 0 estimated mantas and 87 days had $\geq$10. Hithadhoo Corner and Fushi Kandu followed the overall average closely with 0.59$\pm$0.68% (n photos=324824; range=0%-3.05%), 0.52$\pm$0.66% (n photos=76354; range=0%-2.75%) mantas per photo, respectively. Fonadhoo Beyru displayed a higher mean estimated occurrence of mantas, with 0.81$\pm$0.64% estimated per photo (n photos=21303; range=0%-2.4%) and Boduhuraa Beyru a lower mean estimated occurrence of 0.27$\pm$0.39% (n photos=32977; range=0%-1.89%).

The influence five seasonal predictors (season, moon, chlorophyll-a, temperature and current) had on the estimated number of mantas per photo were analysed through Gaussian GLMs (Supp.Table.1). Monsoon season was shown to significantly affect manta presence (F_2=18.47; $P<0.01$), with higher presence during the SW monsoon and least during the NE monsoon (Fig.2; Fig.3). The specific cleaning sites showed significant differences in the estimated number of mantas (F_3=5.70; $P<0.01$), with higher rates of estimated mantas per photo at Fonadhoo Beyru and Hithadhoo Corner (Fig.3). There was a significant interaction between the season and site (F_6=2.22; P=0.03), indicating these general statistics significantly differ spatiotemporally (Fig.3). Likelihood ratio tests support the inclusion of the interactive term as being significant improvements to the model fit ($\chi^2_1<0.01$; P=0.03).
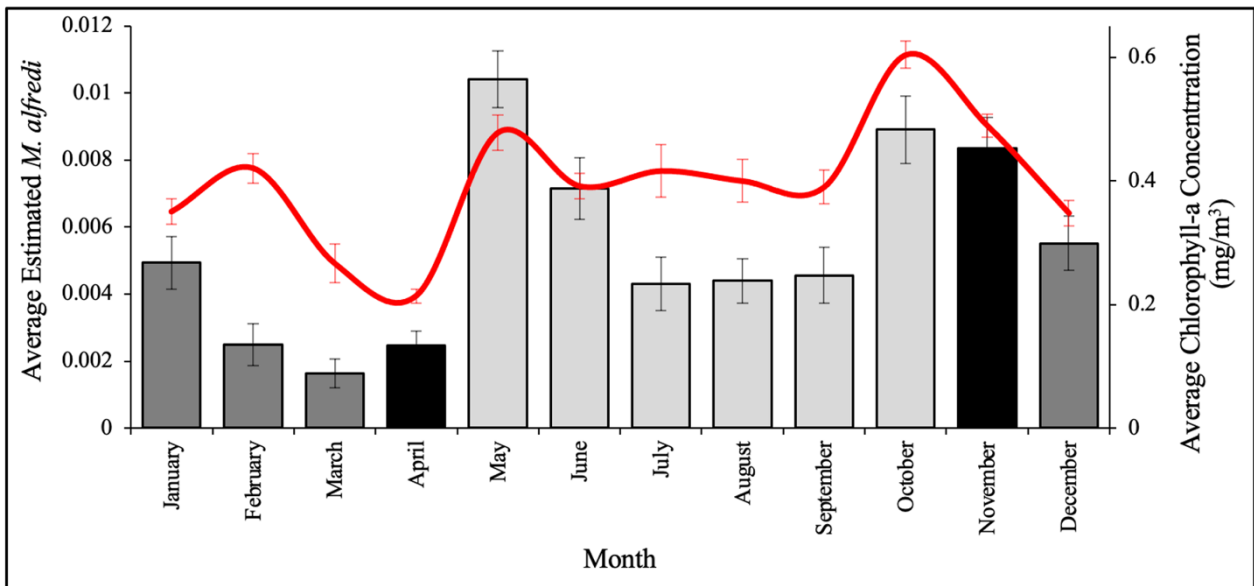
Figure 2 – Average estimated *Mobula alfredi* per photo (bar) and average chlorophyll-a concentration (mg/m^3; red line) for each month. Colours represent monsoon season; May – October: southwest, December – March: northeast and April and November monsoonal retreat.

Additionally, moon state was also found to significantly influence of estimated manta abundance per photo (F_3=9.67; P<0.01). An EMM pairwise comparison showed first-quarter moons had significantly higher rates of estimated mantas present in photos than other states (P<0.01; Fig.4; Supp.Table.2). Other pairwise comparisons returned non-significant (P>0.05; Fig.4; Supp.Table.2). Chlorophyll-a concentration was a significant predictor of the estimated number of mantas per photo (F_1=50.47; P<0.01; Fig.2). As the concentration of chlorophyll-a increases, so did the number of mantas during each season (Fig.2). Temperature displayed a generally homogenous pattern at Hithadhoo Corner and Fushi Kandu. Sampling effort varied between the two sites with 395 data points from Hithadhoo Corner and 34 at Fushi Kandu. Temperature range also varied from 32.1^{o}C to 25.3^{o}C at Hithadhoo Corner, and 32.0^{o}C to 28.3^{o}C at Fushi Kandu. Temperature deviation was small and remained consistent around the mean with a standard deviation of 1.0^{o}C (Hithadhoo Corner mean=29.4^{o}C; Fushi Kandu mean=29.6^{o}C). The second GLM with the inclusion of temperature noted temperature to be a non-significant predictor of manta abundance (F_1=0.05; P=0.82).
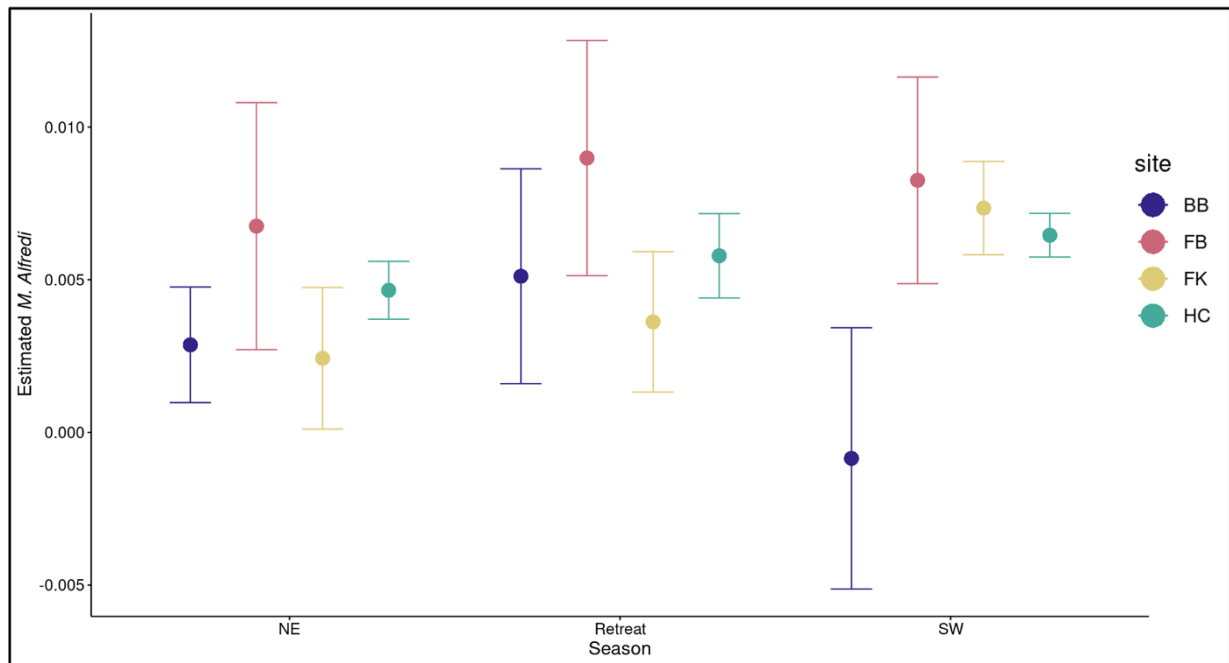
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Figure 3 – Predicted means (dots) and 95% confidence levels (whiskers) for the significant interaction between season and site on the estimated number of *Mobula alfredi* per photo. Predicted values generated through the 'emmeans' package on R, for the Gaussian GLM: Estimated manta per photo ~ season * site + chlorophyll-a + moon phase. Boduhuraa Beyru (BB - Purple); Fonadhoo Beyru (FB - Red); Fushi Kandu (FK - Yellow); Hithadhoo Corner (HC - Green).

3.3 Diurnal Variation

Diurnal variation in manta presence was analysed to understand temporal drivers of day-time abundance. Overall, 80.1% of hours had a sum maxN of 0 and 16.5% had a maxN of ≥ 2. These varied spatially, with Hithadhoo Corner having its highest maxN of 4, and a mean maxN of 0.3±0.7 per hour (n hours=6,047). Fushi Kandu, Fonadhoo Beyru and Boduhuraa Beyru had peak maxN and mean maxN per hour of 4, 5, and 3 and 0.29±0.76, 0.45±0.81 and 0.14±0.46, respectively (n hours=1416; 1809; 647, respectively). Boduhuraa Beyru expressed the highest recorded maxN of 5 mantas and Fushi Kandu for the highest sum maxN per hour on two occasions of 8.
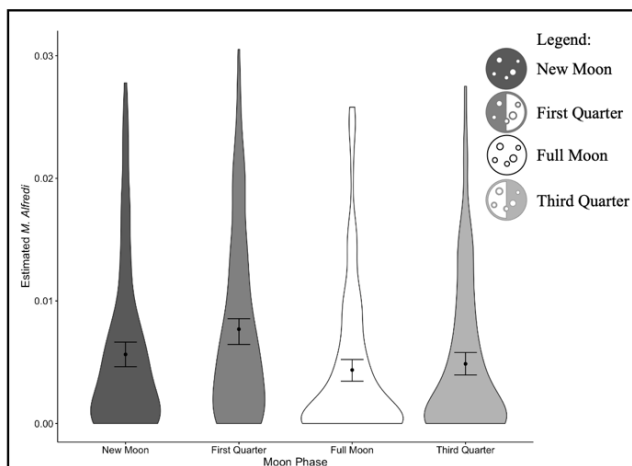

Figure 4– The effect of moon state on the estimated *Mobula alfredi* per photo. Dots represent the mean and whiskers the 95% confidence interval.

Hour categories surveyed ranged from 5:00 to 19:00 and a Gaussian GLM showed hour to significantly impact manta maxN (F_{14}=24.15; P<0.01; Fig.5; Supp.Table.3). Between 8:00
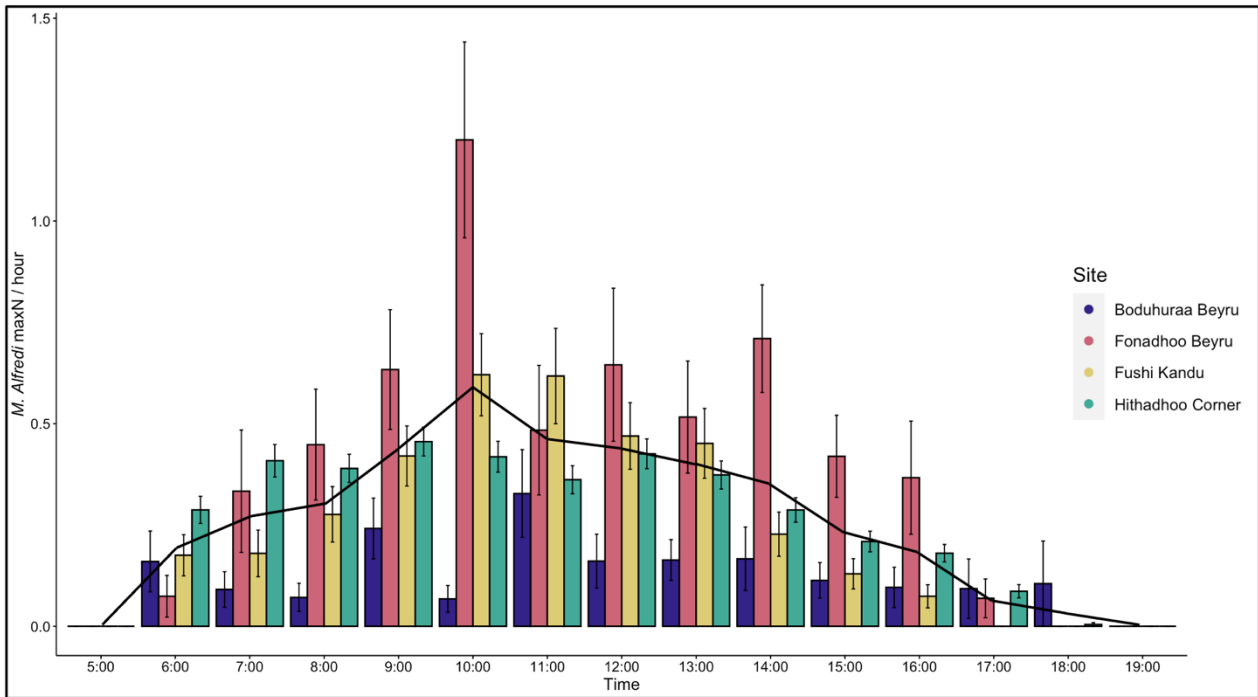
Figure 5 – The mean maxN of *Mobula alfredi* for each hour interval at each site; Boduhuraa Beyru (Purple), Fonadhoo Beyru (Red), Fushi Kandu (Yellow) and Hithadhoo Corner (Green). The black line is the collective mean average for all the sites.

and 13:00 is the period cleaning was highest (Fig.5). An EMM post hoc test revealed 09:00 and 10:00 had significantly higher abundances of mantas than 05:00, 06:00 and 14:00 onwards and non-significantly higher abundance than 07:00, 08:00 and 11:00 to 13:00 (Supp.Fig.4; Supp.Table.4). Although all sites seem to display reduced maxN outside of this window, it seems maxN at Fonadhoo Beyru remained high until 16:00, unlike the other three sites which demonstrate a drop in maxN from 13:00 (Fig.5).

Human presence varied, with between 7:00 and 11:00 having the highest average peaks in human maxN. Although the highest maxN per frame was 11 humans at Hithadhoo Corner in April 2023, 98.5% of photos contained 0. Between sites, the mean human per photo, per hour for Hithadhoo Corner, Fushi Kandu and Fonadhoo Beyru was 0.04±0.40, 0.03±0.42, and 0.03±0.32, respectively. Boduhuraa Beyru was the site with the fewest photos per hour with humans present, with a mean of 0.01±0.12. The GLM revealed hourly human maxN to non-significantly affect manta presence (F_1=1.22; P=0.26). The tide state was also a non-significant predictor (F_3=1.61; P=0.33). Although there was a slight increase in abundance during the flood (mean=0.35±0.77) and low tide

(mean=0.31±0.74), the difference to the ebb (mean=0.24±0.59) and high tide (mean=0.29±0.69) was marginal. The short deployment of the TCM-x current meters at Hithadhoo Corner returned speed (F_1=3.08; P=0.07) and heading (F_1=0.22; P=0.63) to be non-significant predictors of manta presence.

Finally, a GLM identified manta maxN to significantly affect their sighting duration (F_1=276.35; P<0.01; Fig.6; Supp.Table.5). Sighting durations varied, with encounters of >2 hours apparent on eight days. Mean sighting durations at Fonadhoo Beyru (7.21±22.15 minutes) were larger than those elsewhere (Hithadhoo Corner:1.93±8.19; Fushi Kandu:1.42±6.15; Boduhuraa Beyru:0.93±4.83, minutes). All sites displayed positive correlations, although at Hithadhoo Corner, Fushi Kandu and Boduhuraa Beyru, strong positive trends were observed, indicating when there are more mantas, they spend more time at these cleaning sites (Fig.6).
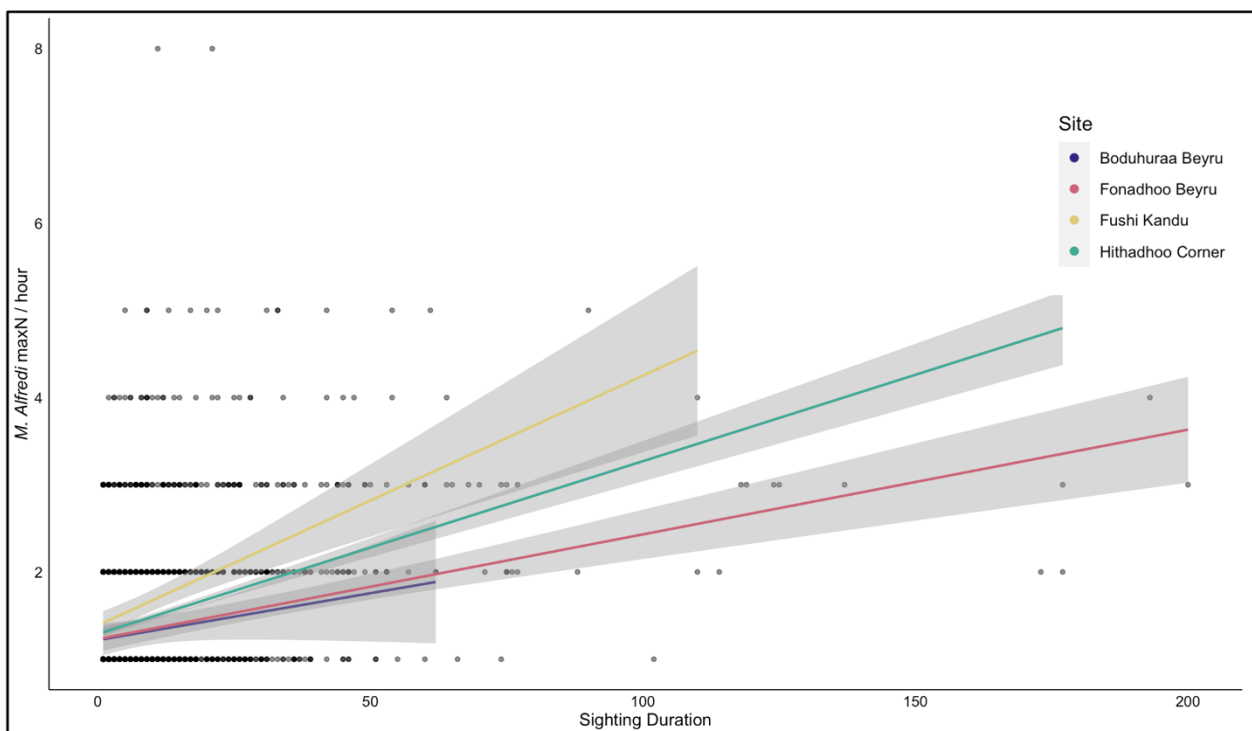

Figure 6 – The effect of *Mobula aflredi* maxN on sighting duration at each site; Boduhuraa Beyru (Purple), Fonadhoo Beyru (Red), Fushi Kandu (Yellow) and Hithadhoo Corner (Green). Regression lines plotted using Linear Models. Grey shading represents the standard error.

3.4 Residency

Repeated identification of mantas provides powerful insights into residency patterns and social demographics. Successful identification was possible on 629 occasions, consisting of 81 unique individuals, more than half of all those ever identified around Laamu (n=144). 10 of these were sighted only once and 45 sighted ≥5 times. MV-MA-3004 was identified 33 times, more than any other individual. On 23 occasions, the individual could not be identified. Generally, 24.2% of estimated mantas were successfully identified. The quality of images varied at each site, with the few deployments at Fonadhoo Beyru being particularly successful, whereby 60.5% of estimated mantas were identified and Fushi Kandu the opposite, with only 15.12% identified. There was a near-even sex split with a slight female bias, with 50.6% of all unique individuals female, 46.9% male and 2.5% of unknown sex. Maturity consisted of 64.2% adult, 29.6% juvenile, 3.7% subadult and 2.5% unknown. All sites displayed their importance for multiple demographic classes, particularly Hithadhoo Corner, where 33.3% of individuals sighted were juvenile (n=69).

Sighting interval times varied spatiotemporally (Fig.7). The mean number of days between sightings for individuals sighted ≥2 times was 62.32±4.04 days (n mantas=71), with MV-MA-2552 having the longest interval between sightings of 519 days. Mean intervals between sightings tended to decrease as the number of sightings increased. The mean sighting interval for a second sighting was 100.36±121.74 days which had a large range of 379 days. An individual's sighting interval decreased to 28.62±30.5 days by their 9th sighting (n mantas=29) and the lowest interval, which applied to 10 individuals was 12.3±13.49 days on their 20th sighting, suggesting some individuals stayed in proximity to the cleaning stations. The mean sighting interval for mantas sighted on multiple occasions was 352.65±260.48 days but individually varied (Fig.7). The longest interval from the first sighting on 5th January 2021 to the final sighting on 18th May 2023 was a period of 747 days for manta MV-MA-3754, which was sighted 23 times at Hithadhoo Corner only. Contrastingly, MV-MA-
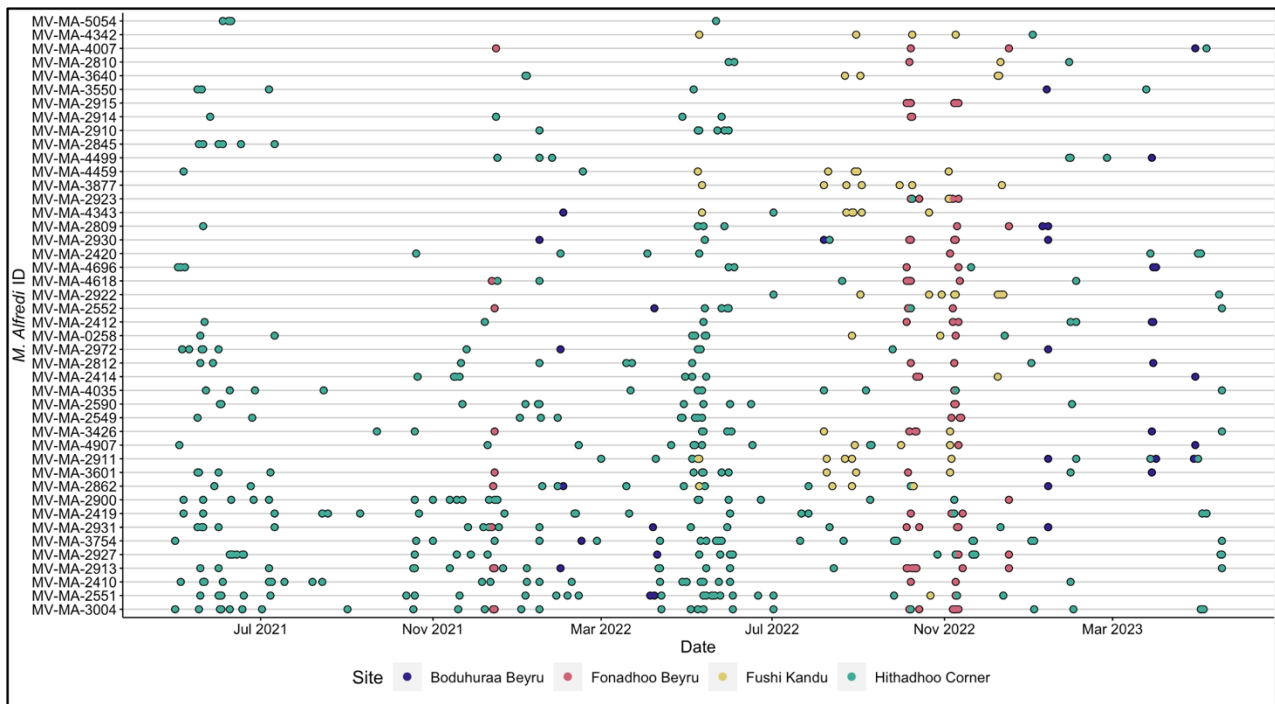
Figure 7 – Identified *Mobula alfredi* sightings throughout the survey period for individuals sighted five or more times. Point colour represents site identified; Boduhuraa Beyru (BB; Purple), Fonadhoo Beyru (FB; Red), Fushi Kandu (FK; Yellow) and Hithadhoo Corner (HC; Green).

3755 was only sighted twice between 9th June 2021 and 10th June 2021 in Hithadhoo Corner and has not been sighted since. Intra-specific variation in periodicity was clear. For example, MV-MA-2900 and MV-MA-2927 seem to occupy cleaning sites more seasonally, whereas MV-MA-2551 and MV-MA-2862 display more consistent patterns of annual residency (Fig.7). Multiple site use was apparent for 53 individuals (74.64%; n=71) with evident inter-atoll migrations occurring in short time frames (Fig.7). For example, MV-MA-2862 was sighted at Hithadhoo Corner on 8th October 2022 and two days later at Fushi Kandu, a ~30km inter-atoll migration (Fig.7).

4. Discussion

4.1 Drivers of Abundance

4.1.1 Annual Productivity

The world's largest monsoonal variation (Su *et al.* 2021) significantly affected manta presence at cleaning stations around Laamu. Previous studies from elsewhere in the Maldives archipelago are in support of southwest winds increasing presence (Anderson *et al.* 2011a; Stevens 2016; Harris *et al.* 2020). Chlorophyll-a concentration, and the predicted association with zooplankton, was another

significant variable affecting manta presence which complements oceanographic upwelling theories (Doty & Oguri 1956; Harris *et al.* 2020; Su *et al.* 2021). Southwest winds drive leeward upwellings (Harris *et al.* 2020). In Laamu, the leeward northwest of the atoll is where Fushi Kandu is which could explain the seasonal increase in presence here. Increased cleaning station attendance during periods of high productivity has been attributed to reduced time-seeking productive areas (Barr & Abelson 2019). Therefore there is more time for cleaning site visitation, increased need for gill raker cleaning and post-foraging thermoregulation from periods spent in deep, cool waters (Soares *et al.* 2011; Thorrold *et al.* 2014; Knochel *et al.* 2022). Mantas at Fushi Kandu fell during the northeast monsoon, suggesting presence at this site is driven by foraging.

Throughout the atoll, presence declined during the northeast monsoon. The productivity of the northeast monsoon is considered lower than the southwest monsoon via the input of low-salinity surface waters from the Bay of Bengal, inhibiting nutrient-rich upwellings (Bruce *et al.* 1994; Schulte *et al.* 1999). This implies mantas must travel further to satisfy forage requirements and frequent cleaning sites less. This indicates a reduced effect of seasonal movements within Laamu, in comparison to the cross-nation migration observed further north (Harris *et al.* 2020). Seasonal presence at Hithadhoo Corner does not follow hypotheses suggested for the Maldives (Harris *et al.* 2020) and other archipelagos in the Indian Ocean (Peel *et al.* 2019b). Annually high presence here may indicate the importance of this site for other life history endeavours. The lack of appreciation for Boduhuraa Beyru and Fonadhoo Beyru is due to the inconsistent deployment of RUPs throughout different seasons, making it challenging to draw reliable conclusions. The southwest monsoon is one of particular importance in the Maldives, lasting for six months and consequently boasting a prolonged period of productivity (Stevens 2016). Stevens (2016) also indicates the importance of the monsoon retreat for social interaction and ultimately copulation, where observed courtship displays increased in March, October, and November, whereby high fitness from a productive season lends to

an increase in reproductive effort (Harris *et al.* 2020). High chlorophyll-a and abundance around cleaning sites in the months prior to November in Laamu may suggest these theories apply here.

Cleaning site interconnectedness shown by short-interval resighting suggests the cost of longer travel from productive patches to ones that provide superior cleaning services as well as social interactions may be beneficial (Stevens 2016), explaining the high annual abundance at Hithadhoo Corner. Cleaner fish service is suggested to improve with an increase in intra-specific competition (Adam 2010). Larger cleaning stations, like Hithadhoo Corner, support a higher density of cleaner territories, positively influencing intra-specific competition and therefore improving manta cleaning service. The size of the station may also directly influence social interactions and have an increased station capacity (Stevens *et al.* 2018). Our findings show an increase in manta presence positively influences sighting duration at all four sites and displays the importance of cleaning stations for social interactions around Laamu regardless of size.

4.1.2 Diurnal Visitation

The analysis of fine-scale parameters raised suggestions on diurnal spatial patterns. Manta presence in our study supports others that have holistic temporal understandings (Dewar *et al.* 2008; Graham *et al.* 2012; Rohner *et al.* 2013; Andrzejaczek *et al.* 2019; Murie *et al.* 2020). Peak abundance at 09:00 and 10:00 is comparable with Andrzejaczek *et al.*, (2020) and Knochel *et al.* (2022) who found presence to peak at 12:00 in Hawaii and 08:30 in Sudan, respectively, which raises questions as to whether the mantas in Laamu display reverse diel vertical migration (DVM).

Zooplankton DVM is a well-studied concept (Wickstead 1976; Hays 2003). Zooplankton seeks deeper depths during daylight hours and shallower depths at night to graze on phytoplankton (Wickstead 1976; Bezerra-Neto *et al.* 2009). Our results have day-time similarity with others that

quantified diurnal presence and absence with high-resolution satellite (Graham *et al.* 2012; Braun *et al.* 2015) and acoustic telemetry (Clark 2010; Peel *et al.* 2020). These studies suggest mantas are driven by zooplankton DVM and the day-time presence are comparable to Laamu. This is also explained by the dietary plasticity mantas express (Peel *et al.* 2019a). Surface feeding during the day, observed inconsistently in Laamu (The Manta Trust, *Pers. Comm.*), and deep foraging at night have been identified elsewhere by stable isotope analysis (Peel *et al.* 2019a) and multi-function data loggers (Jaine *et al.* 2014). The use of cleaning stations opportunistically during this diurnal change in foraging sites has been suggested (Peel *et al.* 2019a) and could provide explanations for the patterns found in our study. Additionally, daytime cleaning could explain this, since services are optimised when cleaner *Labroides sp.* are most active and visual inter-specific cues from clients to initiate cleaning can be reciprocated (Slobodkin & Fishelson 1974; Côté 2000; Rohner *et al.* 2013).

The significant interaction of the moon state on abundance in this study supports theories of reverse DVM (Lassauce *et al.* 2022). The general increase in presence during low illumination moon states has been found in numerous studies, both within the Maldives (Harris & Stevens 2021) and elsewhere (Couturier *et al.* 2018; Barr & Abelson 2019; Peel *et al.* 2019b). Zooplankton DVM is more coordinated during darker nights and the predation-grazing trade-off for the zooplankton threshold remains deeper during the full moon (Parra *et al.* 2019). Reduced abundances at cleaning stations around Laamu during the full moon may require longer or deeper periods of foraging with the energetic requirement to return to clean being too high (Dewar *et al.* 2008; Andrzejaczek *et al.* 2020).

The lack of effect tide and current found in our study may be indicative of adequate foraging opportunities. It is possible that reliance on fine-scale environmental factors to increase patch densities, as populations in BIOT do (Harris *et al.* 2021), are absent in Laamu. Other studies' results support the need to accurately quantify current, as it may affect cleaner wrasse activity, sediment suspension and cleaning energy expenditure (Rohner *et al.* 2013; Barr & Abelson 2019; Harris *et al.*

2021). However short deployments of current meters at Hithadhoo Corner, during the northeast monsoon when presence was lowest, may have contributed to inconclusive data, so continued effort is needed here. Furthermore, the non-significant effect of temperature on presence was expected, considering the narrow range of temperatures recorded. Furthermore, previous studies showed temperature to be a less influential environmental driver of manta presence (Jaine *et al.* 2012). As highlighted by Palacios *et al.* (2023) it is necessary to identify individual temperature profiles to draw conclusive insights into in-situ measurements.

4.2 Residency

Over half of the previously identified mantas were successfully identified around Laamu. Sighting-intervals differed between individuals which provides powerful insights into residential behaviours of the Maldivian sub-population frequently sighted here. Clear year-round sightings were observed for some mantas at multiple sites, while others appeared to exhibit fidelity to single cleaning sites, also shown in Baa Atoll, Maldives (Harris & Stevens 2021) and Raja Ampat, Indonesia (Setyawan *et al.* 2022). This is further supported by a short mean re-sighting interval of 62.3 days which decreased with the number of times an individual was sighted. This indicates that mantas sighted multiple times are often re-sighted and remain in proximity to Laamu. The high sighting rate of juveniles, especially at Hithadhoo Corner, identifies the atoll as important for all demographics. It is out of the scope of this study to determine any site as a nursery ground, but the high prevalence of juveniles could suggest localised breeding (Stevens 2016). The single sighting of some individuals raises the question of a semi-resident local population, with some mantas displaying potentially transient characteristics. Only 36 individuals were sighted less than five times, conservative, when considering that RUP systems fall short of determining absolute absence and had an identification success rate of 24%. Annual multi-demographic residency, copulation and pregnancies have been observed at Hithadhoo Corner (Stevens 2016). Coupled with frequent sightings and local oceanographic features may

suggest Laamu's manta population shows signs of partial isolation from the rest of the Maldivian archipelago.

Variability in residency was expected, and these results are aligned with satellite and telemetry studies which have previously displayed individual differences in fidelity to cleaning sites in Australia (Couturier *et al.* 2018), Indonesia (Germanov & Marshall 2014), and the Red Sea (Braun *et al.* 2015). Within the Maldives, SCUBA-based surveys display cross-atoll migrations of individuals, leaving and returning to Laamu, so it is known that the local population here is not entirely isolated (The Manta Trust, *Pers. Comm.*). Long-distance migrations of 1000km and 505km have been documented in Australia, via archival satellite tags (Jaine *et al.* 2014) and photographic identification in eastern Africa (Marshall *et al.* 2023). Supporting the diverse findings presented here, periods of residency, followed by shorter cross-reef migrations have been found elsewhere (Seychelles: Peel *et al.* 2019b; BIOT: Andrzejaczek *et al.* 2020).

A variety of factors may be driving these differences in abundance, including bathymetry and atoll isolation (Espinoza *et al.* 2016; Peel *et al.* 2019b). Life history needs of the small Laamu manta population may be satisfied by the island mass effect theory and removing their requirement to migrate to other atolls, common elsewhere in the Maldives (Dewar *et al.* 2008; Harris *et al.* 2020). Local bathymetry around Laamu exceeds ~1400m to the north atoll and ~3000m to the south (Rasheed *et al.* 2021). The predation risk associated with deeper water may be too high (Whitney *et al.* 2023), given in-shore conditions around Laamu could be satisfactory year-round. A genetic study on reef manta rays in Hawaii could provide comparisons to these theories. Whitney *et al.*, (2023) concluded two islands, only 46 km apart, have genetically distinct populations of mantas, due to a parting 3000m channel and satisfaction of the island mass effect. Similarly in the Maldives, Hosegood (2020) concluded that five individuals from Laamu and 18 from Baa and Raa atoll, were genetically related and indicate inter-atoll connectedness. Laamu's geographical isolation in comparison to

Hawaii (Whitney et al. 2023) and individual variation in residency in this study and neighbouring BIOT (Andrzejaczek et al. 2020) may indicate partial residency. This suggests that Hosegood's (2020) small sample size may prematurely generalize Laamu. While past studies have shown mesoscale fidelity (Couturier et al. 2018), our research raises questions about Laamu forming discrete populations, like Hawaii, within globally recognized sub-populations (Couturier et al. 2012).

4.3 Study Limitations

The RUP deployments here proved to be effective when compared to traditional SCUBA observations of mantas. Stevens (2016) encountered a comparable 2.7 mantas per survey day compared to the average 3.5 presented here. RUPs are low-cost, non-invasive, easy to deploy and capture unbiased snapshots of time. No published literature has solely used RUPs to study mantas before and our results show how valuable remote observations are. However, combining methodologies, like opportunistic SCUBA and RUP, improves understanding of spatiotemporal ecology, importance, and functioning, as well as providing clear avenues of future research and conservation priorities (Kitchen-Wheeler 2010; Stevens *et al.* 2018; Stewart *et al.* 2018).

This study has some drawbacks, like those of many photographic-based studies (Stewart *et al.* 2018), which intrinsically limit the breadth of inference our results can provide. Sighting events defined by an arbitrary interval of 10 minutes inflate pseudoreplication and therefore the estimated abundance. Accurate identification of intervals between cleaning events, using satellite tags would prove useful. Opposingly, maxN is considered a conservative measure of abundance, although definite (Sherman *et al.* 2018). However, neither count provided insight into absence, a shortfall of many observational techniques. Time of first arrival or maximum individuals (maxIND), and indexes of residency (Graham *et al.* 2012), were all unfeasible given the systems are passive. Here 24.2% of individuals were successfully identified, low when compared to the near 100% success rate SCUBA photographs, remote underwater video and acoustic telemetry have (O'Shea *et al.* 2010; Stevens 2016;

Andrzejaczek *et al.* 2020). This limits direct statistical comparison of the Laamu cleaning sites to others, reducing the credibility of some result inferences. Additionally, the narrow GoPro field of view creates a trade-off; either capturing the whole cleaning station or high-resolution branchial spot images. Systems were placed in favour of quality branchial spot photographs, reducing the quantity of the cleaning station observed. Issues with parallax errors, low-quality images, biofouling, floating debris and partial branchial photographs, further jeopardised identification. Sequeira *et al.*, (2012) rightly highlighted the uncertainty around using chlorophyll-a as a proxy for zooplankton, raising caution over such variables being indirect, weak and delayed. Furthermore, the data used here is of low resolution and did not allow for site-specific values to be obtained.

Our results should not be disregarded, considering the ease of access and use of such data in the past (Anderson *et al.* 2011a; Jaine *et al.* 2014; Cabral *et al.* 2023). For improved inter-atoll interpretation, future research should endeavour to take in-situ zooplankton samples or invest in higher-resolution data, such as hyperspectral imaging (Zhang *et al.* 2022). The proximity of Hithadhoo Corner to Six Senses resort, created a high degree of sampling bias towards this site. This made direct comparisons and a full understanding of specific inter-atoll drivers of presence difficult to conclude upon. Financial and logistical restraints further compromised exploratory dive prospects to identify new cleaning sites which provide uncertainty as to whether the four cleaning sites in this study provide a representative sample of manta abundances for the atoll. Such limitations will need to be considered for future research and studies using RUP elsewhere. The use of 360º cameras, site exploration and as recommended by Palacios (2023), combining long-term photographic studies with other sampling strategies, may provide a more holistic and conclusive understanding of Laamu's manta population.

4.4 Application and Future Directions

Mantas are one of the least fecund species in the world and listed as vulnerable to extinction (Dulvy *et al.* 2014; Murray *et al.* 2020). Fishing is generally considered their greatest threat (Croll *et al.*

2016). Regional law prohibits the direct capture of manta rays within the Maldives (Maldives EPA 2014). The burgeoning of illegal encroachment from adjacent fisheries (Fernando & Stewart 2021) coupled with mantas diurnal migrations raises concerns whether this species-specific protection is enough. Presence at cleaning stations infrequently exceeded two minutes, so protection must extend further than just these sites. Inferred residency around cleaning sites and potential isolation in Laamu and subsequent vulnerability of this sub-population calls for atoll-specific, marine, and terrestrial legislation.

Land reclamation is common around the Maldives (Pancrazi *et al.* 2020) but the isolation of Laamu has restricted such activities (Stevens & Froman 2018) necessitating precautionary spatiotemporal protection. Furthermore, rises in sea surface temperatures, resulting in increases in Maldivian coral bleaching alerts (Davies 2023) and 20% reductions in zooplankton over the last half-century (Singh *et al.* 2018) highlight the need for urgent local and global reform. Positively, anthropogenic presence proved to non-significantly affect abundance. Although the RUP demonstrated to infrequently capture breaches of the Manta Trust's code of conduct, threats from tourism currently remain low. The necessity and growth of tourism but observed negative effects on mantas in the Maldives (Anderson *et al.* 2011b; O'Malley *et al.* 2013; Murray *et al.* 2020), provide a warning that effective marine protection needs to be gazetted. Laamu presents itself as an oasis amongst an oasis. The designation as a Hope Spot (Mission Blue 2021), for its proven refuge during anthropogenic climate change and housing coral reefs with remarkable recovery to bleaching (Davies 2023), increases the need for adequate marine protection. The local manta population is smaller than others identified in parts of the Maldives (Stevens 2016) and shows signs of isolation. Therefore, the vulnerability and inter-individual reliance are amplified, and there is a clear need for species- and atoll-specific legislation to be designated within Laamu for their protection.

Without management and enforcement, the MPAs in the Maldives are little more than 'paper parks' (Mohamed 2007; Rife *et al.* 2013). Laamu's currently provide no additional protection to the resident manta population, despite being strategically placed. Hithadhoo Island is the first Maldivian community to propose managing their own marine resources, which includes Hithadhoo Corner. Maldives Resilient Reefs, a local non-governmental organisation affiliated with BLUE Marine Foundation, is currently implementing the Community Conservation Area (CCA) designation and drafting the management plan in consultation with the local residents. The importance of community engagement is clear for long-term, sustainable protection (Grorud-Colvert *et al.* 2021). This study has highlighted the annual importance of these cleaning sites and per the MPA guide (Grorud-Colvert *et al.* 2021), it is recommended that highly protected MPAs are designated at all four sites, with fishing, tourism, dredging, and boat use management of high importance. Permanent protection is recommended at Hithadhoo Corner due to its annual importance for cleaning and social interactions (Stevens 2016; Stevens *et al.* 2018). Fonadhoo Beyru and Boduhurra Beyru should be precautionarily protected. Until further study at these sites, long-term importance cannot be inferred, despite the few deployments at Fonadhoo Beyru showing a high presence of mantas. Fushi Kandu, showed seasonal variations, so protection at least during the southwest monsoon, may prove adequate.

A strategic network of connected MPAs is unfeasible due to a lack of insight into spatiotemporal site use. Therefore, considerations for an atoll-wide MPA are suggested, especially as our results infer the importance of the atoll for high annual productivity and presence. Additionally, the implementation and effectiveness of larger MPAs are cost-effective (McCrea-Strub *et al.* 2011). As with the BIOT (Gruby *et al.* 2016), such an MPA would directly protect the mantas, and indirectly the reefs and terrestrial systems, both required to satisfy atoll biogeochemical cycles and manta life histories. Expansions on this study, to identify other key aggregation areas, will further MPA planning specificity and ultimately effectiveness.

Two clear research priorities emerged from our study. *First*: the requirement to identify key forage aggregations. Specific protection must expand further than cleaning stations for this species' longevity. The close affinity tuna fisheries and reef manta rays have with primary productivity (Croll *et al.* 2016), and reports of illegal fishing in Maldivian waters (Fernando & Stewart 2021), puts unknown foraging aggregations at risk. Argos-linked satellite tags, like Wildlife computers Fastloc (Braun *et al.* 2015), will provide accurate insights into the breadth of habitat use, inter-atoll connectivity, nursery grounds and foraging aggregations. *Second*: To what degree the Laamu manta population is isolated from the rest of the Maldives to the north and island nations to the south. Genetic samples will provide such insights and for local prey selection to also be identified via stable isotope analysis. Execution of these research priorities, with continuous SCUBA-based observations, RUP deployment and exploration of Laamu will develop a holistic spatial understanding of the manta population and for marine protection to be warranted and directed.

This study provides a comprehensive understanding of the seasonality around Laamu, with prior literature based on a small sample of fishermen's sightings (Anderson *et al.* 2011a) or a lack of directed attention (Harris *et al.* 2020). Contrary to the rest of the Maldives, Laamu may produce adequate foraging patches annually, which provides important insights into how predicted shifts to phytoplankton assemblages, from climate change, may affect future manta presence. The perturbations mantas are facing globally, and their intrinsic risk of over-exploitation coupled with a fundamental lack of scientific understanding, make effective protection challenging. The continual development of site-specific understanding around important aggregation areas will prove essential for the future persistence of this species.

5. References

Adam, T.C. (2010). Competition encourages cooperation: client fish receive higher-quality service when cleaner fish compete. *Anim. Behav.*, 79, 1183–1189.

Anderson, R.C., Adam, M. & Goes, J. (2011a). From monsoons to mantas: Seasonal distribution of Manta alfredi in the Maldives. *Fish. Oceanogr.*, 20, 104–113.

Anderson, R.C., Adam, M.S., Kitchen-Wheeler, A.-M. & Stevens, G. (2011b). Extent and Economic Value of Manta Ray Watching in Maldives. *Tour. Mar. Environ.*, 7, 15–27.

Andrzejaczek, S., Chapple, T., Curnick, D., Carlisle, A., Castleton, M., Jacoby, D., *et al.* (2020). Individual variation in residency and regional movements of reef manta rays Mobula alfredi in a large marine protected area. *Mar. Ecol. Prog. Ser.*, 639, 137–153.

Andrzejaczek, S., Gleiss, A.C., Pattiaratchi, C.B. & Meekan, M.G. (2019). Patterns and drivers of vertical movements of the large fishes of the epipelagic. *Rev. Fish Biol. Fish.*, 29, 335–354.

Armstrong, A.O., Armstrong, A.J., Bennett, M.B., Richardson, A.J., Townsend, K.A. & Dudgeon, C.L. (2019). Photographic identification and citizen science combine to reveal long distance movements of individual reef manta rays Mobula alfredi along Australia's east coast. *Mar. Biodivers. Rec.*, 12, 14.

Armstrong, A.O., Armstrong, A.J., Jaine, F.R.A., Couturier, L.I.E., Fiora, K., Uribe-Palomino, J., *et al.* (2016). Prey Density Threshold and Tidal Influence on Reef Manta Ray Foraging at an Aggregation Site on the Great Barrier Reef. *PLOS ONE*, 11, e0153393.

Armstrong, A.O., Stevens, G.M.W., Townsend, K.A., Murray, A., Bennett, M.B., Armstrong, A.J., *et al.* (2021). Reef manta rays forage on tidally driven, high density zooplankton patches in Hanifaru Bay, Maldives. *PeerJ*, 9, e11992.

Aslam, M. & Kench, P.S. (2017). Reef island dynamics and mechanisms of change in Huvadhoo Atoll, Republic of Maldives, Indian Ocean. *Anthropocene*, 18, 57–68.

Barr, Y. & Abelson, A. (2019). Feeding – Cleaning Trade-Off: Manta Ray "Decision-Making" as a Conservation Tool. *Front. Mar. Sci.*, 6.

Bezerra-Neto, J., Mello, Barbosa, P. & Pinto-Coelho, R. (2009). The role of predation in the diel vertical migration of zooplankton in two tropical freshwaters ecosystems. *Acta Limnol. Bras.*, 21, 45–56.

Bohorquez, J.J., Dvarskas, A., Jacquet, J., Sumaila, U.R., Nye, J. & Pikitch, E.K. (2022). A New Tool to Evaluate, Improve, and Sustain Marine Protected Area Financing Built on a Comprehensive Review of Finance Sources and Instruments. *Front. Mar. Sci.*, 8.

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. *Mar. Biol.*, 162, 2351–2362.

Bruce, J.G., Johnson, D.R. & Kindle, J.C. (1994). Evidence for eddy formation in the eastern Arabian Sea during the northeast monsoon. *J. Geophys. Res. Oceans*, 99, 7651–7664.

Cabral, M.M.P., Stewart, J.D., Marques, T.A., Ketchum, J.T., Ayala-Bocos, A., Hoyos-Padilla, E.M., *et al.* (2023). The influence of El Niño Southern Oscillation on the population dynamics of oceanic manta rays in the Mexican Pacific. *Hydrobiologia*, 850, 257–267.

Clark, T. (2010). Abundance, home range, and movement patterns of manta rays (Manta alfredi, M. birostris) in Hawai'i. PhD Thesis. University of Hawaii.

Côté, I. (2000). Evolution and ecology of cleaning symbiosis in the sea. In: *Oceanography and Marine Biology, by Gibson. R & Barnes. M*. Taylor and Francis, pp. 311–355.

Couturier, L., Marshall, A., Jaine, F., Kashiwagi, T., Pierce, S., Townsend, K., *et al.* (2012). Biology, ecology and conservation of the Mobulidae. *J. Fish Biol.*, 80, 1075–119.

Couturier, L., Newman, P., Jaine, F., Bennett, M., Venables, W., Cagua, E., *et al.* (2018). Variation in occupancy and habitat use of Mobula alfredi at a major aggregation site. *Mar. Ecol. Prog. Ser.*, 599, 125–145.

Croll, D.A., Dewar, H., Dulvy, N.K., Fernando, D., Francis, M.P., Galván-Magaña, F., *et al.* (2016). Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. *Aquat. Conserv. Mar. Freshw. Ecosyst.*, 26, 562–575.

Davies, R. (2023). Temporal changes in coral reef condition in the Maldives. University of Exeter.

Deakos, M., Baker, J. & Bejder, L. (2011). Characteristics of a manta ray Manta alfredi -population off Maui, Hawaii, and implications for management. *Mar. Ecol. Prog. Ser.*, 429, 245–260.

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. *Mar. Biol.*, 155, 121–133.

Doty, M.S. & Oguri, M. (1956). The Island Mass Effect. *ICES J. Mar. Sci.*, 22, 33–37.

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

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., *et al.* (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506, 216–220.

Espinoza, M., Heupel, M.R., Tobin, A.J. & Simpfendorfer, C.A. (2016). Evidence of Partial Migration in a Large Coastal Predator: Opportunistic Foraging and Reproduction as Key Drivers? *PLOS ONE*, 11, e0147608.

E.U. Copernicus Marine Service Information. (2023). Global Ocean Biogeochemistry Analysis and Forecast. Marine Data Store (MDS).

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

Germanov, E.S. & Marshall, A.D. (2014). Running the Gauntlet: Regional Movement Patterns of Manta alfredi through a Complex of Parks and Fisheries. *PLOS ONE*, 9, e110071.

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., *et al.* (2017). Capacity shortfalls hinder the performance of marine protected areas globally. *Nature*, 543, 665–669.

Graham, R.T., Witt, M.J., Castellanos, D.W., Remolina, F., Maxwell, S., Godley, B.J., *et al.* (2012). Satellite Tracking of Manta Rays Highlights Challenges to Their Conservation. *PLOS ONE*, 7, e36834.

Grorud-Colvert, K., Sullivan-Stack, J., Roberts, C., Constant, V., Horta E Costa, B., Pike, E.P., *et al.* (2021). The MPA Guide: A framework to achieve global goals for the ocean. *Science*, 373, eabf0861.

Gruby, R.L., Gray, N.J., Campbell, L.M. & Acton, L. (2016). Toward a Social Science Research Agenda for Large Marine Protected Areas. *Conserv. Lett.*, 9, 153–163.

Grutter, A.S. (1996). Experimental demonstration of no effect by the cleaner wrasse Labroides dimidiatus (Cuvier and Valenciennes) on the host fish Pomacentrus moluccensis (Bleeker). *J. Exp. Mar. Biol. Ecol.*, 196, 285–298.

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

Harris, J.L., McGregor, P.K., Oates, Y. & Stevens, G.M.W. (2020). Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (Mobula alfredi) in the Maldives, implications for conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.*, 30, 1649–1664.

Harris, J.L. & Stevens, G.M.W. (2021). Environmental drivers of reef manta ray (Mobula alfredi) visitation patterns to key aggregation habitats in the Maldives. *PLOS ONE*, 16, e0252470.

Hay, M.E., Parker, J.D., Burkepile, D.E., Caudill, C.C., Wilson, A.E., Hallinan, Z.P., *et al.* (2004). Mutualisms and Aquatic Community Structure: The Enemy of My Enemy Is My Friend. *Annu. Rev. Ecol. Evol. Syst.*, 35, 175–197.

Hays, G.C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations.

Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.*, 23, 202–210.

Hosegood, J. (2020). Genomic Tools for Conservation and Management of Manta and Devil Rays (Mobula Spp.). *PQDT - UK Irel.* PhD Thesis. .

Jaine, F., Rohner, C., Weeks, S., Couturier, L., Bennett, M., Townsend, K., *et al.* (2014). Movements and habitat use of reef manta rays off eastern Australia: offshore excursions, deep diving and eddy affinity revealed by satellite telemetry. *Mar. Ecol. Prog. Ser.*, 510, 73–86.

Jaine, F.R.A., Couturier, L.I.E., Weeks, S.J., Townsend, K.A., Bennett, M.B., Fiora, K., *et al.* (2012). When Giants Turn Up: Sighting Trends, Environmental Influences and Habitat Use of the Manta Ray Manta alfredi at a Coral Reef. *PLOS ONE*, 7, e46170.

Jorgensen, S., Micheli, F., White, T., Van Houtan, K., Alfaro-Shigueto, J., Andrzejaczek, S., *et al.* (2022). Emergent research and priorities for shark and ray conservation. *Endanger. Species Res.*, 47, 171–203.

Kashiwagi, T., Marshall, A.D., Bennett, M.B. & 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. *Mar. Biodivers. Rec.*, 4, e53.

Kitchen-Wheeler, A.-M. (2010). Visual identification of individual manta ray (*Manta alfredi*) in the Maldives Islands, Western Indian Ocean. *Mar. Biol. Res.*, 6, 351–363.

Knochel, A.M., Hussey, N.E., Kessel, S.T., Braun, C.D., Cochran, J.E.M., Hill, G., *et al.* (2022). Home sweet home: spatiotemporal distribution and site fidelity of the reef manta ray (Mobula alfredi) in Dungonab Bay, Sudan. *Mov. Ecol.*, 10, 22.

Lamouroux, J., Perruche, C., Mignot, A., Paul, J. & Szczypta, C. (2022). *Quality Information Document for Global Biogeochemical Analysis and Forecast Product. GLOBAL_ANALYSIS_FORECAST_BIO_001_028.*

Lassauce, H., Dudgeon, C., Armstrong, A., Wantiez, L. & Carroll, E. (2022). Evidence of fine-scale genetic structure for reef manta rays Mobula alfredi in New Caledonia. *Endanger. Species Res.*, 47, 249–264.

Lenth, R.V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., *et al.* (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means.

Link, J.S. & Watson, R.A. (2019). Global ecosystem overfishing: Clear delineation within real limits to production. *Sci. Adv.*, 5, eaav0474.

MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., *et al.* (2020). Global status and conservation potential of reef sharks. *Nature*, 583, 801–806.

Maldives EPA. (2014). *Batoidea Maldives Protection. 438-ECAS/438/2014/81.*

Manta Trust. (2022). *Impact Report 2022.*

Marshall, A., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M., *et al.* (2022). Mobula alfredi (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2022: e.T195459A214395983.

Marshall, A.D., Flam, A.L., Cullain, N., Carpenter, M., Conradie, J. & Venables, S.K. (2023). Southward range extension and transboundary movements of reef manta rays Mobula alfredi along the east African coastline. *J. Fish Biol.*, 102, 628–634.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. & Warner, R.R. (2015). Marine defaunation: Animal loss in the global ocean. *Science*, 347, 1255641.

McCrea-Strub, A., Zeller, D., Rashid Sumaila, U., Nelson, J., Balmford, A. & Pauly, D. (2011). Understanding the cost of establishing marine protected areas. *Mar. Policy*, 35, 1–9.

Mission Blue. (2021). *Mission Blue: Annual Report 2021.*

Mohamed, M. (2007). Economic valuation of coral reefs: A case study of the costs and benefits of improved management of Dhigali Haa, a marine protected area in Baa atoll, Maldives. University of Canterbury.

Murie, C., Spencer, M. & Oliver, S.P. (2020). Current strength, temperature, and bodyscape modulate cleaning services for giant manta rays. *Mar. Biol.*, 167, 54.

Murray, A., Garrud, E., Ender, I., Lee-Brooks, K., Atkins, R., Lynam, R., *et al.* (2020). Protecting the million-dollar mantas; creating an evidence-based code of conduct for manta ray tourism interactions. *J. Ecotourism*, 19, 132–147.

O'Malley, M.P., Lee-Brooks, K. & Medd, H.B. (2013). The Global Economic Impact of Manta Ray Watching Tourism. *PLOS ONE*, 8, e65051.

O'Shea, O.R., Kingsford, M.J. & Seymour, J. (2010). Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef. *Mar. Freshw. Res.*, 61, 65.

Palacios, M.D., Stewart, J.D., Croll, D.A., Cronin, M.R., Trejo-Ramírez, A., Stevens, G.M.W., *et al.* (2023). Manta and devil ray aggregations: conservation challenges and developments in the field. *Front. Mar. Sci.*, 10.

Pancrazi, I., Ahmed, H., Cerrano, C. & Montefalcone, M. (2020). Synergic effect of global thermal anomalies and local dredging activities on coral reefs of the Maldives. *Mar. Pollut. Bull.*, 160, 111585.

Parra, S.M., Greer, A.T., Book, J.W., Deary, A.L., Soto, I.M., Culpepper, C., *et al.* (2019). Acoustic detection of zooplankton diel vertical migration behaviors on the northern Gulf of Mexico shelf. *Limnol. Oceanogr.*, 64, 2092–2113.

Parton, K.J., Doherty, P.D., Parrish, M., Shearer, P., Myrick, K., Shipley, O.N., *et al.* (2023). Opportunistic camera surveys provide insight into discrete foraging behaviours in nurse sharks (Ginglymostoma cirratum). *Environ. Biol. Fishes*, 106, 19–30.

Peel, L.R., Daly, R., Keating Daly, C.A., Stevens, G.M.W., Collin, S.P. & Meekan, M.G. (2019a). Stable isotope analyses reveal unique trophic role of reef manta rays (*Mobula alfredi*) at a remote coral reef. *R. Soc. Open Sci.*, 6, 190599.

Peel, L.R., Stevens, G.M.W., Daly, R., Daly, C.A.K., Lea, J.S.E., Clarke, C.R., *et al.* (2019b). Movement and residency patterns of reef manta rays Mobula alfredi in the Amirante Islands, Seychelles. *Mar. Ecol. Prog. Ser.*, 621, 169–184.

Peel, L.R., Stevens, G.M.W., Daly, R., Keating Daly, C.A., Collin, S.P., Nogués, J., *et al.* (2020). Regional Movements of Reef Manta Rays (Mobula alfredi) in Seychelles Waters. *Front. Mar. Sci.*, 7.

Potts, G.W. (1973). The ethology of Labroides dimidiatus (cuv. & val.) (Labridae, Pisces) on Aldabra. *Anim. Behav.*, 21, 250–291.

Rasheed, S., Warder, S.C., Plancherel, Y. & Piggott, M.D. (2021). Response of tidal flow regime and sediment transport in North Malé Atoll, Maldives, to coastal modification and sea level rise. *Ocean Sci.*, 17, 319–334.

Rife, A.N., Erisman, B., Sanchez, A. & Aburto-Oropeza, O. (2013). When good intentions are not enough … Insights on networks of "paper park" marine protected areas: Concerns regarding marine "paper parks." *Conserv. Lett.*, 6, 200–212.

Roberts, K.E., Valkan, R.S. & Cook, C.N. (2018). Measuring progress in marine protection: A new set of metrics to evaluate the strength of marine protected area networks. *Biol. Conserv.*, 219, 20–27.

Rohner, C., Pierce, S., Marshall, A., Weeks, S., Bennett, M. & Richardson, A. (2013). Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. *Mar. Ecol. Prog. Ser.*, 482, 153–168.

Saltzman, J. & White, E.R. (2022). *Determining the Role of Environmental Covariates on Planktivorous Elasmobranch Population Trends within an Isolated Marine Protected Area* (preprint). Ecology.

Schulte, S., Rostek, F., Bard, E., Rullkötter, J. & Marchal, O. (1999). Variations of oxygen-minimum and primary productivity recorded in sediments of the Arabian Sea. *Earth Planet. Sci. Lett.*, 173, 205–221.

Sequeira, A., Mellin, C., Rowat, D., Meekan, M.G. & Bradshaw, C.J.A. (2012). Ocean-scale prediction of whale shark distribution. *Divers. Distrib.*, 18, 504–518.

Setyawan, E., Stevenson, B.C., Erdmann, M.V., Hasan, A.W., Sianipar, A.B., Mofu, I., *et al.* (2022). Population estimates of photo-identified individuals using a modified POPAN model reveal that Raja Ampat's reef manta rays are thriving. *Front. Mar. Sci.*, 9.

Sherman, C.S., Chin, A., Heupel, M.R. & Simpfendorfer, C.A. (2018). Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? *J. Exp. Mar. Biol. Ecol.*, 503, 80–85.

Singh, A.D., Jung, S.J.A., Anand, P., Kroon, D. & Ganeshram, R.S. (2018). Rapid switch in monsoon-wind induced surface hydrographic conditions of the eastern Arabian Sea during the last deglaciation. *Quat. Int.*, Reconstruction of the Late Quaternary Asian monsoonal intensity using marine and lake sediment cores, 479, 3–11.

Slobodkin, L.B. & Fishelson, L. (1974). The Effect of the Cleaner-Fish Labroides dimidiatus on the Point Diversity of Fishes on the Reef Front at Eilat. *Am. Nat.*, 108, 369–376.

Sluka, R.D. (2000). Grouper and Napoleon Wrasse ecology in Laamu Atoll, Republic of Maldives: Part 2. Timing, location, and characteristics of spawning aggregations. *Atoll Res. Bull.*, 492, 1–15.

Soares, M.C., Oliveira, R.F., Ros, A.F.H., Grutter, A.S. & Bshary, R. (2011). Tactile stimulation lowers stress in fish. *Nat. Commun.*, 2, 534.

Stevens, G. & Froman, N. (2018). The Maldives Archipelago. In: *World seas: an environmental evaluation: volume II: the Indian Ocean to the Pacific* (ed. Sheppard, C.). London: Academic Press, pp. 211–236.

Stevens, G.M.W. (2016). Conservation and Population Ecology of Manta Rays in the Maldives.

Stevens, G.M.W., Hawkins, J.P. & Roberts, C.M. (2018). Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives. *J. Fish Biol.*, 93, 344–359.

Stewart, J.D., Jaine, F.R.A., Armstrong, A.J., Armstrong, A.O., Bennett, M.B., Burgess, K.B., *et al.* (2018). Research Priorities to Support Effective Manta and Devil Ray Conservation. *Front. Mar. Sci.*, 5.

Strike, E.M., Harris, J.L., Ballard, K.L., Hawkins, J.P., Crockett, J. & Stevens, G.M.W. (2022). Sublethal Injuries and Physical Abnormalities in Maldives Manta Rays, Mobula alfredi and Mobula birostris. *Front. Mar. Sci.*, 9.

Su, D., Wijeratne, S. & Pattiaratchi, C.B. (2021). Monsoon Influence on the Island Mass Effect Around the Maldives and Sri Lanka. *Front. Mar. Sci.*, 8.

Thorrold, S.R., Afonso, P., Fontes, J., Braun, C.D., Santos, R.S., Skomal, G.B., *et al.* (2014). Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nat. Commun.*, 5, 4274.

Venables, S., McGregor, F., Brain, L. & Van Keulen, M. (2016). Manta ray tourism management, precautionary strategies for a growing industry: a case study from the Ningaloo Marine Park, Western Australia. *Pac. Conserv. Biol.*, 22, 295.

Venegas, R.M., Acevedo, J. & Treml, E.A. (2023). Three decades of ocean warming impacts on marine ecosystems: A review and perspective. *Deep Sea Res. Part II Top. Stud. Oceanogr.*, 105318.

Whitney, J.L., Coleman, R.R. & Deakos, M.H. (2023). Genomic evidence indicates small island-resident populations and sex-biased behaviors of Hawaiian reef Manta Rays. *BMC Ecol. Evol.*, 23, 31.

Wickstead, J.H. (John H. (1976). *Marine zooplankton*. The Institute of Biology's studies in biology. Edward Arnold.

Zhang, J., Fu, P., Meng, F., Yang, X., Xu, J. & Cui, Y. (2022). Estimation algorithm for chlorophyll-a concentrations in water from hyperspectral images based on feature derivation and ensemble learning. *Ecol. Inform.*, 71, 101783.

END OF MAIN TEXT

6. Supplementary Materials

6.1 Supplementary Figures
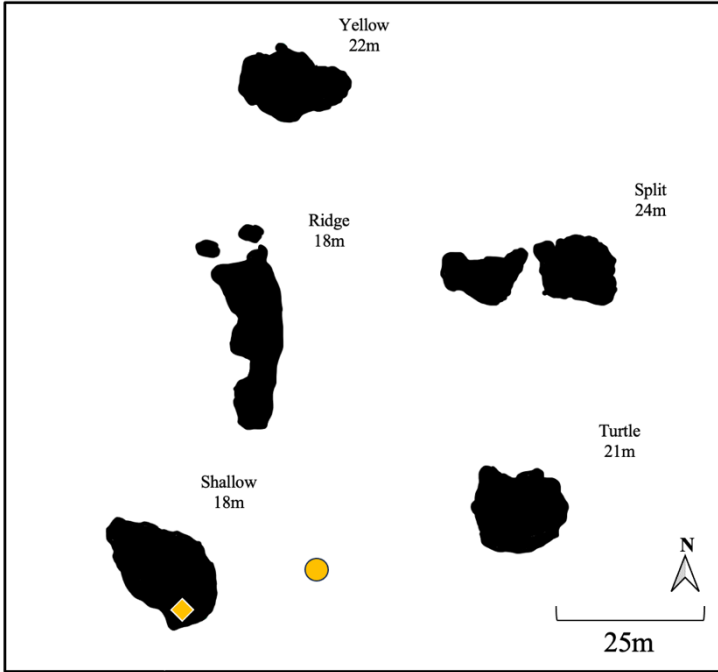
Supplementary Figure 1 – Diagram of Hithadhoo Corner cleaning stations. Yellow circle represents the TCM-x current meter deployment locations and yellow diamond the RUP system deployment location.
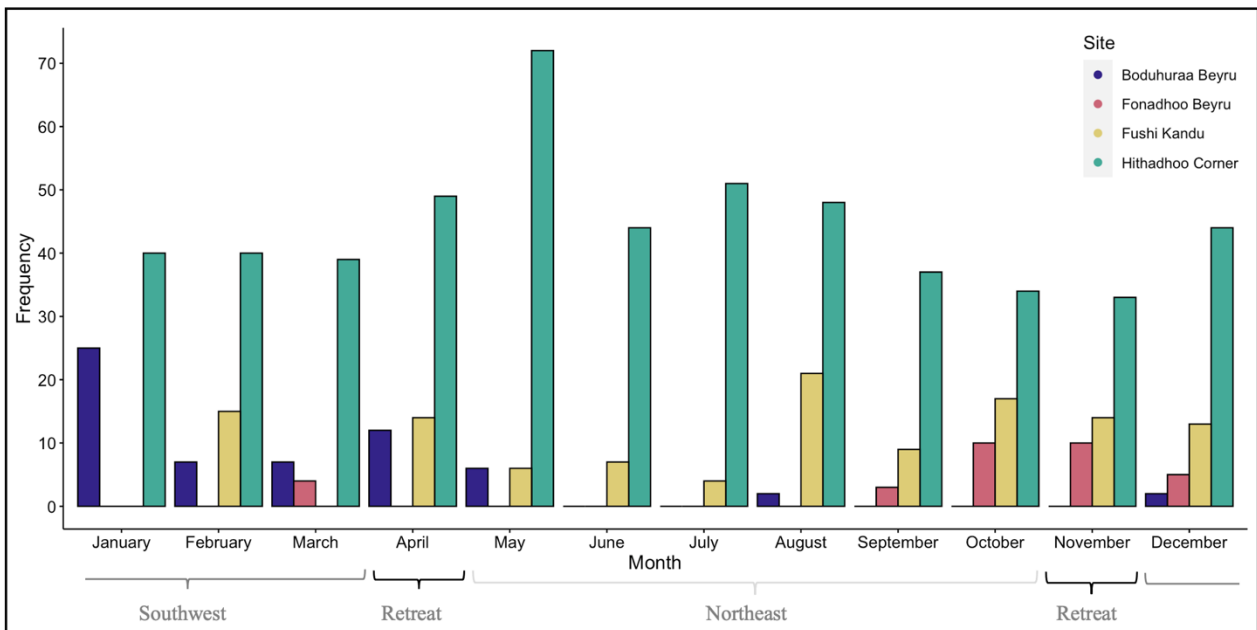
Supplementary Figure 2 – Cumulative survey days per month and season for each site; Boduhuraa Beyru (Purple), Fonadhoo Beyru (Red), Fushi Kandu (Yellow) and Hithadhoo Corner (Green).
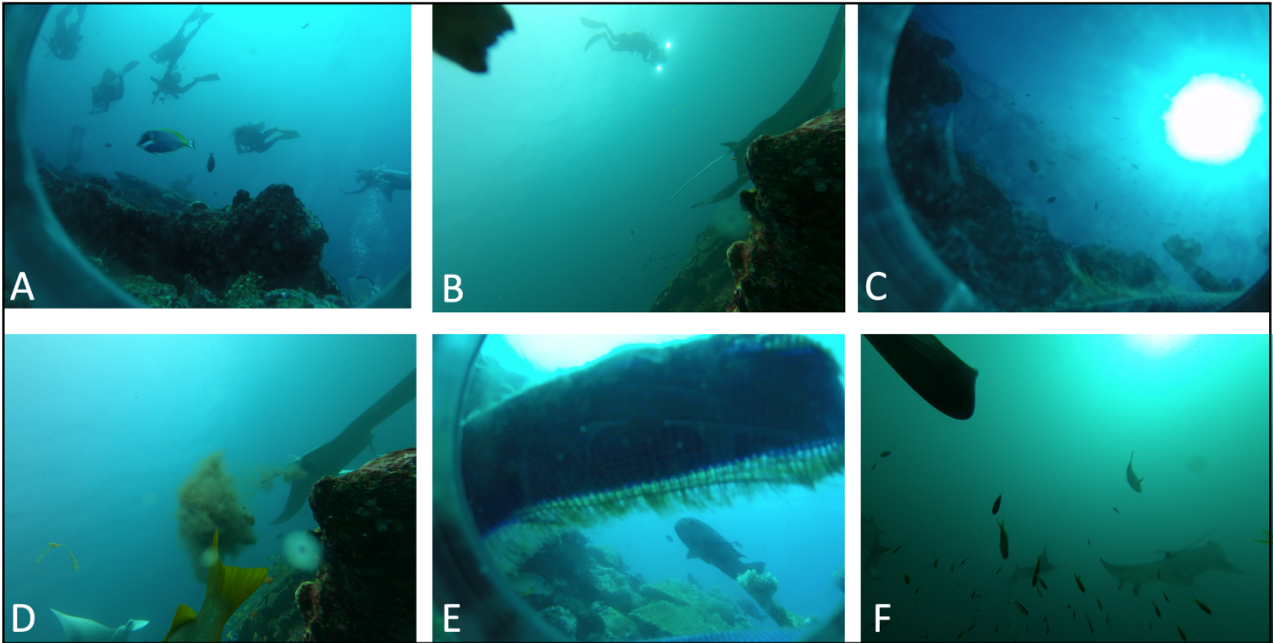
Supplementary Figure 3 – **A)** Nine divers breaching the Manta Trust code of conduct, by swimming over a cleaning station at Hithadhoo Corner, 30th April 2023; **B)** Human – *Mobula alfredi* interaction at Hithadhoo Corner, 16th May 2023; **C)** Negative effects of biofouling on field of view and glare; **D)** *Mobula alfredi* defecating on Hithadhoo Corner, Shallow Block, 17th May 2023; **E)** Physical obstruction from loose housing strap; **F)** Perceived social interaction of *Mobula alfredi*.
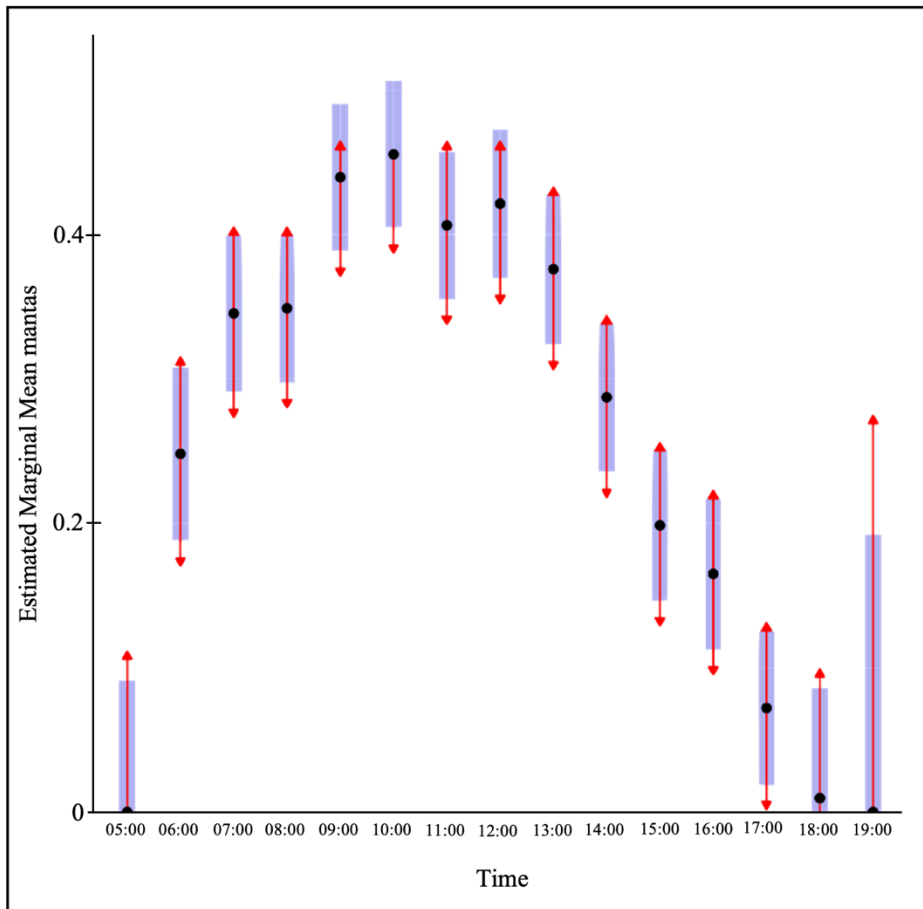
Supplementary Figure 4: Summary of estimated marginal means post hoc test, identifying the times that significantly affect *Mobula alfredi* maxN per hour. Black dots are means, purple boxes are the 95% confidence intervals and red arrows are a scheme to determine homogenous groups. If the arrows overlap the groups are not significantly different from one another.

6.2 Supplementary Tables

Supplementary Table 1: Summary of two Gaussian GLMs. **A)** Estimated *Mobula alfredi* per photo per deployment ~ season * site + chlorophyll-a (chla) + moon. **B)** Estimated *Mobula alfredi* per photo per deployment ~ season * site + chlorophyll-a (chla) + moon + temp. Note: temperature data was only gathered at Hithadhoo Corner and Fushi Kandu.

A — Full Gaussian GLM model, excl. temperature

	Variable	Estimate	Std..Error	t.value	P.value
1	(Intercept)	0.002	0.001	1.568	0.117
2	moonFull Moon	-0.003	0.001	-4.121	0.00004
3	moonNew Moon	-0.002	0.001	-2.990	0.003
4	moonThird Quarter	-0.002	0.001	-3.290	0.001
5	seasonRetreat	0.002	0.002	1.113	0.266
6	seasonSW	-0.004	0.002	-1.554	0.121
7	siteFB	0.004	0.002	1.705	0.089
8	siteFK	-0.0004	0.002	-0.289	0.773
9	siteHC	0.002	0.001	1.661	0.097
10	chla	0.007	0.001	6.920	0
11	seasonRetreat:siteFB	-0.00002	0.003	-0.005	0.996
12	seasonSW:siteFB	0.005	0.004	1.455	0.146
13	seasonRetreat:siteFK	-0.001	0.003	-0.406	0.685
14	seasonSW:siteFK	0.009	0.003	3.096	0.002
15	seasonRetreat:siteHC	-0.001	0.002	-0.509	0.611
16	seasonSW:siteHC	0.006	0.002	2.242	0.025

AIC: -5387.8; R2: 0.17

B — Full Gaussian GLM model, incl. temperature

	Variable	Estimate	Std..Error	t.value	P.value
1	(Intercept)	0.007	0.009	0.755	0.451
2	moonFull Moon	-0.004	0.001	-4.496	0.00001
3	moonNew Moon	-0.003	0.001	-3.503	0.001
4	moonThird Quarter	-0.004	0.001	-4.271	0.00002
5	seasonRetreat	0.003	0.002	1.177	0.240
6	seasonSW	0.012	0.004	3.206	0.001
7	siteHC	0.003	0.002	2.097	0.037
8	chla	0.006	0.001	4.939	0.00000
9	temp	-0.0002	0.0003	-0.618	0.537
10	seasonRetreat:siteHC	-0.0004	0.002	-0.150	0.881
11	seasonSW:siteHC	-0.011	0.004	-3.108	0.002

AIC: - 3145.6; R2: 0.17]

Supplementary Table 2: Summary of significant estimated marginal means pairwise posthoc test, identifying the moon phases that significantly affect *Mobula alfredi* maxN per hour, with Bonferroni adjustment.

Pairwise Comparisons of Moon Phases

	contrast	estimate	SE	df	z.ratio	p.value
1	First quarter - Full moon	0.455	0.115	Inf	3.945	0.0005
2	First quarter - New moon	0.347	0.110	Inf	3.149	0.010
3	First quarter - Third quarter	0.378	0.117	Inf	3.241	0.007
4	Full moon - New moon	-0.108	0.126	Inf	-0.854	1
5	Full moon - Third quarter	-0.077	0.129	Inf	-0.597	1
6	New moon - Third quarter	0.031	0.125	Inf	0.249	1

Supplementary Table 3: Summary of a Gaussian GLM minimum adequate model identifying the diurnal factors affecting *Mobula alfredi* maxN per hour category. *Mobula alfredi* maxN per hour ~ Hour. Tide state, temperature, current speed, current heading and human maxN per hour were all nonsignificant predictors.

Diurnal Gaussian GLM Minimum Adequate model

	Variable	Estimate	Std.Error	tValue	PValue
1	(Intercept)	0	0.047	0	1
2	time6:00	0.248	0.056	4.455	0.00001
3	time7:00	0.345	0.054	6.377	0
4	time8:00	0.349	0.053	6.535	0
5	time9:00	0.440	0.053	8.256	0
6	time10:00	0.455	0.053	8.560	0
7	time11:00	0.406	0.053	7.626	0
8	time12:00	0.421	0.053	7.890	0
9	time13:00	0.376	0.054	7.024	0
10	time14:00	0.287	0.053	5.372	0.00000
11	time15:00	0.199	0.054	3.707	0.0002
12	time16:00	0.165	0.054	3.074	0.002
13	time17:00	0.072	0.054	1.336	0.181
14	time18:00	0.010	0.061	0.158	0.874
15	time19:00	0	0.109	0	1

AIC: 17758; R2: 0.033

Supplementary Table 4: Summary of significant estimated marginal means pairwise posthoc test, identifying the times that significantly affect *Mobula alfredi* maxN per hour, with Bonferroni adjustment.

Contrast	Estimate	SE	DF	t.ratio	P.value
5:00 - 6:00	-0.25	0.06	8488	-4.46	<.0001
5:00 - 7:00	-0.35	0.05	8488	-6.38	<.0001
5:00 - 8:00	-0.35	0.05	8488	-6.54	<.0001
5:00 - 9:00	-0.44	0.05	8488	-8.26	<.0001
5:00 - 10:00	-0.46	0.05	8488	-8.56	<.0001
5:00 - 11:00	-0.41	0.05	8488	-7.63	<.0001
5:00 - 12:00	-0.42	0.05	8488	-7.89	<.0001
5:00 - 13:00	-0.38	0.05	8488	-7.02	<.0001
5:00 - 14:00	-0.29	0.05	8488	-5.37	<.0001
5:00 - 15:00	-0.20	0.05	8488	-3.71	0.0222
6:00 - 9:00	-0.19	0.04	8488	-4.78	0.0002
6:00 - 10:00	-0.21	0.04	8488	-5.18	<.0001
6:00 - 11:00	-0.16	0.04	8488	-3.94	0.0085
6:00 - 12:00	-0.17	0.04	8488	-4.30	0.0018
6:00 - 17:00	0.18	0.04	8488	4.30	0.0018
6:00 - 18:00	0.24	0.05	8488	4.82	<.0001
7:00 - 15:00	0.15	0.04	8488	3.83	0.0138
7:00 - 16:00	0.18	0.04	8488	4.69	<.0001
7:00 - 17:00	0.27	0.04	8488	7.04	<.0001
7:00 - 18:00	0.34	0.05	8488	7.04	<.0001
8:00 - 15:00	0.15	0.04	8488	4.03	0.0058
8:00 - 16:00	0.18	0.04	8488	4.92	<.0001
8:00 - 17:00	0.28	0.04	8488	7.34	<.0001
8:00 - 18:00	0.34	0.05	8488	7.25	<.0001
9:00 - 14:00	0.15	0.04	8488	4.12	0.004
9:00 - 15:00	0.24	0.04	8488	6.50	<.0001
9:00 - 16:00	0.27	0.04	8488	7.38	<.0001
9:00 - 17:00	0.37	0.04	8488	9.79	<.0001
9:00 - 18:00	0.43	0.05	8488	9.21	<.0001
9:00 - 19:00	0.44	0.10	8488	4.33	0.0016
10:00 - 14:00	0.17	0.04	8488	4.56	<.0001
10:00 - 15:00	0.26	0.04	8488	6.94	<.0001
10:00 - 16:00	0.29	0.04	8488	7.82	<.0001
10:00 - 17:00	0.38	0.04	8488	10.23	<.0001
10:00 - 18:00	0.45	0.05	8488	9.56	<.0001
10:00 - 19:00	0.46	0.10	8488	4.49	<.0001
11:00 - 15:00	0.21	0.04	8488	5.60	<.0001
11:00 - 16:00	0.24	0.04	8488	6.48	<.0001
11:00 - 17:00	0.33	0.04	8488	8.89	<.0001
11:00 - 18:00	0.40	0.05	8488	8.49	<.0001
11:00 - 19:00	0.41	0.10	8488	4.00	0.0066
12:00 - 14:00	0.13	0.04	8488	3.61	0.0327
12:00 - 15:00	0.22	0.04	8488	5.97	<.0001
12:00 - 16:00	0.26	0.04	8488	6.85	<.0001
12:00 - 17:00	0.35	0.04	8488	9.25	<.0001
12:00 - 18:00	0.41	0.05	8488	8.79	<.0001
12:00 - 19:00	0.42	0.10	8488	4.15	0.0036
13:00 - 15:00	0.18	0.04	8488	4.73	<.0001
13:00 - 16:00	0.21	0.04	8488	5.61	<.0001
13:00 - 17:00	0.30	0.04	8488	8.01	<.0001
13:00 - 18:00	0.37	0.05	8488	7.80	<.0001
13:00 - 19:00	0.38	0.10	8488	3.70	0.0228
14:00 - 17:00	0.22	0.04	8488	5.69	<.0001
14:00 - 18:00	0.28	0.05	8488	5.92	<.0001
15:00 - 18:00	0.19	0.05	8488	4.02	0.0062

Supplementary Table 5: Summary of a Gaussian GLM looking to identify the effect *Mobula alfredi* maxN per hour has on sighting duration. *M. alfredi* maxN per hour ~ sighting duration.

GLM Model Coefficients

	Estimate	Std. Error	t value	Pr(> | t|)
(Intercept)	-1.979	0.834	-2.373	0.018
manta	8.128	0.489	16.624	0

AIC: 14284; R2: 0.14

END OF ASSESMENT