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Population demographics, habitat use and regional movements of reef manta rays (*Mobula alfredi)* in Makunudhoo, Maldives and implications for management

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Copyright Statement

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Executive Summary

The Republic of Maldives, in the central Indian Ocean, is home to one of the largest known populations of reef manta rays (*Mobula alfredi*). Recognised as one of the ocean's most charismatic megafauna, a developing tourism industry has made them particularly vulnerable to anthropogenic disturbance as a result of poorly managed ecotourism. It is characteristic for subpopulations to aggregate in "hotspots" to feed, clean or engage in social or reproductive activities. Habitat use is often associated with the South Asian monsoon, where individuals seasonally migrate to areas following ocean productivity due to their reliance on prey density. The predictable spatio-temporal distribution of populations, coupled with their conservative life histories, facilitate their vulnerability to tourism exploitation (e.g. direct injury, altered aggregation behaviour) and can hinder long-term survivorship.

Distribution and movement patterns of *M. alfredi* in more remote northern atolls are under researched. Here, photographic identification (photo-ID) records of natural ventral marking patterns were collected in Makunudhoo, Haa Dhaalu Atoll, to investigate their presence in this north-western region. Sightings data was collected at 21 sites across the atoll between 2022 and 2023, in months that reflected the north-east (NE) monsoon (December to April). The number of sightings and individuals were used to assess population demographics; habitat use; site affinity; and regional movements. Boosted regression tree (BRT) modelling was also used to assess the relative influence of, and interaction between temporal predictor variables (hour of the day, day of the year) and moon illumination on sighting probability in the atoll.

A total of 1289 *M. alfredi* sightings were recorded at 17 different sites. Of 323 individuals identified in this study, 240 (74.3%) were new identifications, and 83 (25.7%) were previously documented. The rate of new identifications over the survey period suggests the size of the subpopulation exceeds the number of individuals identified in this study. Demographic data revealed that the majority of the subpopulation was made up of adult males (26.6%) and juvenile females (29.1%); suggesting that Makunudhoo is an important nursery area. A total of six key aggregation sites (>100 sightings) were identified, five of which were appointed important feeding areas and one of which was classified as a cleaning station. Same sight resightings occurred between one and eight times by 243 individuals, demonstrating a variation in site affinity among individuals and between sites. Inter-atoll movement was assessed, revealing that the majority of previously documented individuals were first sighted in Baa Atoll (≈ 134 km away). Ultimately, BRT modelling demonstrated that the probability of sightings was mostly influenced by day of the year (63.2%). A positive interaction effect between temporal predictor variables demonstrated that sightings are most likely to peak in January between 0800-1100.

This is the first photo-ID study conducted on *M. alfredi* in Makunudhoo Atoll. Findings related to the subpopulation's demography, key areas of habitat use, and movement patterns will help to inform species management in light of imminent tourism expansion. Understanding the use of this atoll, particularly by juveniles, can both validate the need for their protection in the form of Marine Protected Areas (MPAs), and highlight priority areas made aware by this study. Data can also be used to help inform regulations specific to the region, and to the species, inspiring more comprehensive management in future development plans.

Impact Summary

This project was completed collaboratively with the Manta Trust, a UK registered charity, with a mission to use research, education and collaboration to conserve mobulids and their associated coral reef habitats. More specifically, the focus of this study is to work alongside and use data from the Maldives Manta Conservation Programme (MMCP). The programme has developed a photo-ID database, cataloguing all *M. alfredi* in the Maldives archipelago, currently supporting the largest population documented to date.

Multi-decadal studies on this population have given insight into the distribution, movement, and habitat use of *M. alfredi*, and the environmental variables that influence their presence. However, studies are often concentrated on subpopulations that exist in central atolls in areas of high tourism activity. As a result, little is known about individuals that occupy more remote northern atolls, leaving entire subpopulations unidentified. This project was the first to investigate *M. alfredi* in Makunudhoo Atoll, located in the north-west of the Maldivian archipelago, for which no photo-ID records have ever been collected. The study will provide baseline data for individuals frequenting Makunudhoo by investigating their habitat use and movement patterns, which will help illustrate the significance of this atoll for the subpopulation.

Plans have been secured to develop a tourist resort and build an airport on the island of Makunudhoo, which is currently very low in tourism activity, and only the secondary contributor to the island's economy following fishing. Improving our understanding of the region's significance to *M. alfredi*, can be used to recommend and enhance environmental management plans. This can ensure impending development and tourism activities remain sustainable and will minimise disturbance to key habitats identified in this study. Recognising Makunudhoo's holistic importance to marine megafauna, may also aid in its establishment as a marine sanctuary or biosphere reserve for which it is fully capable. More specifically, the Manta Trust can use elements of this study to inform the government on ways to manage Makunudhoo as a developing tourist destination, to relieve pressure from unregulated tourism, one of the biggest threats currently facing the Maldivian *M. alfredi* population. For example, understanding habitat use, at specific temporal scales, especially for specific demographics, can inform policies that protect individuals when they are at their most vulnerable.

The MMRP can use findings from this study to add to the current knowledge of the Maldivian *M. alfredi* population, helping to calculate more accurate population estimates, and to hypothesise habitat connectivity between subpopulations. Holistic and broadscale understanding of species ecology is important in any context for the improvement of conservation legislation. Continuing to investigate unidentified subpopulations can help illustrate the necessity for more MPA designations and ensure better protection of a species that is not solely important for its ecological functions but also for its contributions to local economies. Ultimately, this study shows the value of using photo-ID to monitor the presence of *M. alfredi*, and how that can be used to inform regional management of this vulnerable species.

1. Introduction

1.1 Species Ecology

Reef manta rays (*Mobula alfredi*) are large, reef-associated, pelagic elasmobranchs of the Mobulidae family (mobulids), which is comprised of nine species (Harris *et al*., 2020; White *et al*., 2017). They have a circumglobal distribution, and are found in the tropical and sub-tropical waters of the Indo-West Pacific Oceans (Couturier *et al*., 2012; Stevens, 2016). They frequent coastal reef systems, remote oceanic islands (Kashiwagi *et al.*, 2011) and even travel into offshore mesopelagic zones (Braun *et al.*, 2014; Harris *et al*., 2020). Mobulids are characterised by their highly specialised filter-feeding behaviour, which is important for ecosystem functioning. Consumption of fish spawn, zooplankton and other fishes (Couturier *et al.,* 2012) facilitates the horizontal transfer of nutrients to higher trophic levels, which means their conservation is important for protecting ecosystem services like nutrient cycling (Papastamatiou *et al.,* 2015).

1.2 Movement Ecology and Habitat Use

Movement patterns of *M. alfredi* are often associated with resource requirements, related to conditions of high primary productivity and prey density (Jaine *et al.,* 2012; Kitchen-Wheeler, 2010). It has been suggested that *M. alfredi* are highly philopatric, demonstrating high levels of residency and site fidelity, where individuals often repeatedly return to the same areas (Couturier *et al.*, 2011). Their minimal inter-atoll movement suggests that some regional populations are limited to geographic atolls (Kitchen-Wheeler & Edwards, 2011). *Mobula alfredi* are also characterised by their aggregation behaviour. Large numbers (>20) of individuals concentrate in “hotspot” locations and use shallow reefs as feeding areas; as cleaning stations where, cleaner fishes remove parasites; and to engage in intraspecies social and reproductive interactions (Harris *et al.*, 2020; Jaine *et al.*, 2014; Stevens, 2016).

The Maldivian *M. alfredi* population undergoes a seasonal migration influenced by the South Asian monsoon (Anderson, Adam & Goes, 2011). The biannual reversal of winds and associated changing ocean currents triggers an upwelling of nutrients which creates optimal conditions for phytoplankton blooms (Charpy-Roubaud, Charpy & Larkum, 2001). The south-west (SW) monsoon (April - November) brings productivity to the shallow reefs of the eastern side of the atolls and the north-east (NE) monsoon (December - March) enhances productivity to the western side of the atolls; *M. alfredi* follow this productivity to exploit rich feeding grounds (Harris *et al.*, 2020; Harris & Stevens, 2021).

1. 3 Threats to *M. alfredi*

Mobula alfredi are an example of highly conspicuous, charismatic marine megafauna that have gained particular attention in recent years (Davidson *et al.*, 2012). Their role as important flagship species, deemed as beautiful or impressive (Sequeira *et al.*, 2019), and reliable occurrence, has made their conservation more tangible through ecotourism. Despite the economic value brought to local economies (Anderson *et al.,* 2010), the Maldivian *M. alfredi* population is still impacted by unregulated tourism and associated habitat degradation (Rohner *et al.*, 2013).

Disturbance to key habitats has been found to influence aggregation behaviour, resulting in population declines (Venables *et al.,* 2016). For example, *M. alfredi* have been observed abandoning feeding areas in the presence of visitors (Murray *et al.,* 2020). It has been suggested that displacement from feeding areas can lead to reducing fecundity and offspring survival whereas displacement from cleaning stations, where reproductive activity is known to occur, can likely impact breeding success (Stevens, 2016; Venables *et al.,* 2016). Exposure to boat activity can also increase susceptibility to entanglement by fishing gear, propeller injuries and boat strikes with a potential to cause lethal and sublethal injuries (Stevens & Froman, 2018). Tourist activities, like snorkelling or diving, can equally cause direct physical damage to coral reefs and accelerate habitat degradation. A resulting reduction in live coral cover can lessen the abundance of reef fish (Jones *et al.,* 2004) and reduce *M. alfredi* visitation (Barr & Abelson, 2019). The known seasonal migration patterns of this species, means their spatiotemporal distributions are often predictable, and in turn, make them more susceptible to over exploitation by the tourism industry (Harris *et al.,* 2020).

Mobulids are considered as large-bodied animals with slow life-history traits. Their low fecundity, slow growing and late to mature nature makes it particularly difficult for populations to recover from depletion (Dulvy *et al.*, 2014). Population declines of *M. alfredi* in recent decades has led to their classification as Vulnerable to extinction on the IUCN Red List of Threatened Species (Harris *et al.,* 2020; Marshall *et al.,* 2019). Although they are protected from target fisheries in the Republic of Maldives, tourist-led activities continue to put regional populations at risk (EPA, 2014). Currently, Hanifaru Marine Protected Area (MPA) remains one of few protected areas in the Maldives that uses comprehensive management and actively enforces regulations aimed at reducing anthropogenic disturbance to *M. alfredi* aggregation areas (Harris *et al.*, 2020).

1.4 Scope of Research

In the last two decades, photographic identification (photo-ID), acoustic telemetry and satellite tagging studies have been conducted on *M. alfredi* subpopulations in an attempt to understand population structure, movement patterns, spatiotemporal distribution and habitat use throughout Maldivian atolls (Couturier *et al.*, 2011; Harris *et al.*, 2020; Kitchen-Wheeler, Ari, & Edwards, 2011). However, less of these patterns are known about subpopulations which frequent more remote, data poor atolls, like the one identified in this study, Makunudhoo, Haa Dhaalu Atoll. Field observations made prior to this study, observed large numbers of *M. alfredi* occupying this area, suggesting its potential importance as an aggregation area, and is what prompted data collection (T Sawers 2022, personal communication, 2nd December).

1.5 Aims and Objectives

This study aims to understand the significance of Makunudhoo for *M. alfredi* and investigate their spatial ecology within the region. Findings can be used to inform regional management for future touristic development and instigate protection to critical habitats identified in this study.

Recently collected photo-ID records combined with temporal data will be used to:
(1) summarise the number of sightings of *M. alfredi* in Makunudhoo; (2) identify the number of individuals present and investigate the number of new and previously documented individuals; (3) investigate whether all individuals in the subpopulation have been discovered; (4) investigate subpopulation demographics (sex and maturity); (5) assess site visitation to determine key aggregation areas; (6) identify primary site activities to determine habitat uses (7) investigate site affinity in relation to regional movement and resighting events; (8) investigate inter-atoll connectivity and habitat use by assessing movements from previously documented individuals and determine distances travelled; (9) determine whether temporal (day and time) variables, or moon illumination, influence *M. alfredi* presence.

2. Methods

2.1 Study Area

Makunudhoo is located in the northwest of the Maldives archipelago, in the central Indian Ocean and Bay of Bengal (Figure 1). For administrative purposes, it is recognised as part of the Haa Dhaalu Atoll (HDh), located 18 km to the east, but actually forms its own atoll. Makunudhoo is long and narrow in shape, small in size, and spans approximately 27 km in length and 8 km in width (Musthafa, 2013; SOGREAH Consultants & Water Solutions, 2007). The atoll is geographically isolated from the main Maldivian atoll chains; one of its four islands is the most westwardly inhabited island in the country. It maintains a unified reef system oriented in a north-south-west direction and is surrounded by open sea. The western side of the atoll is protected by reefs whereas the eastern side is exposed to north-east winds (SOGREAH Consultants & Water Solutions, 2007). The inside of the atoll, which makes up one single lagoon, reaches a depth up to 70 m (GEBCO, 2023). Only two MPAs exist in Hdh, none of which occur in Makunudhoo (Figure S1).

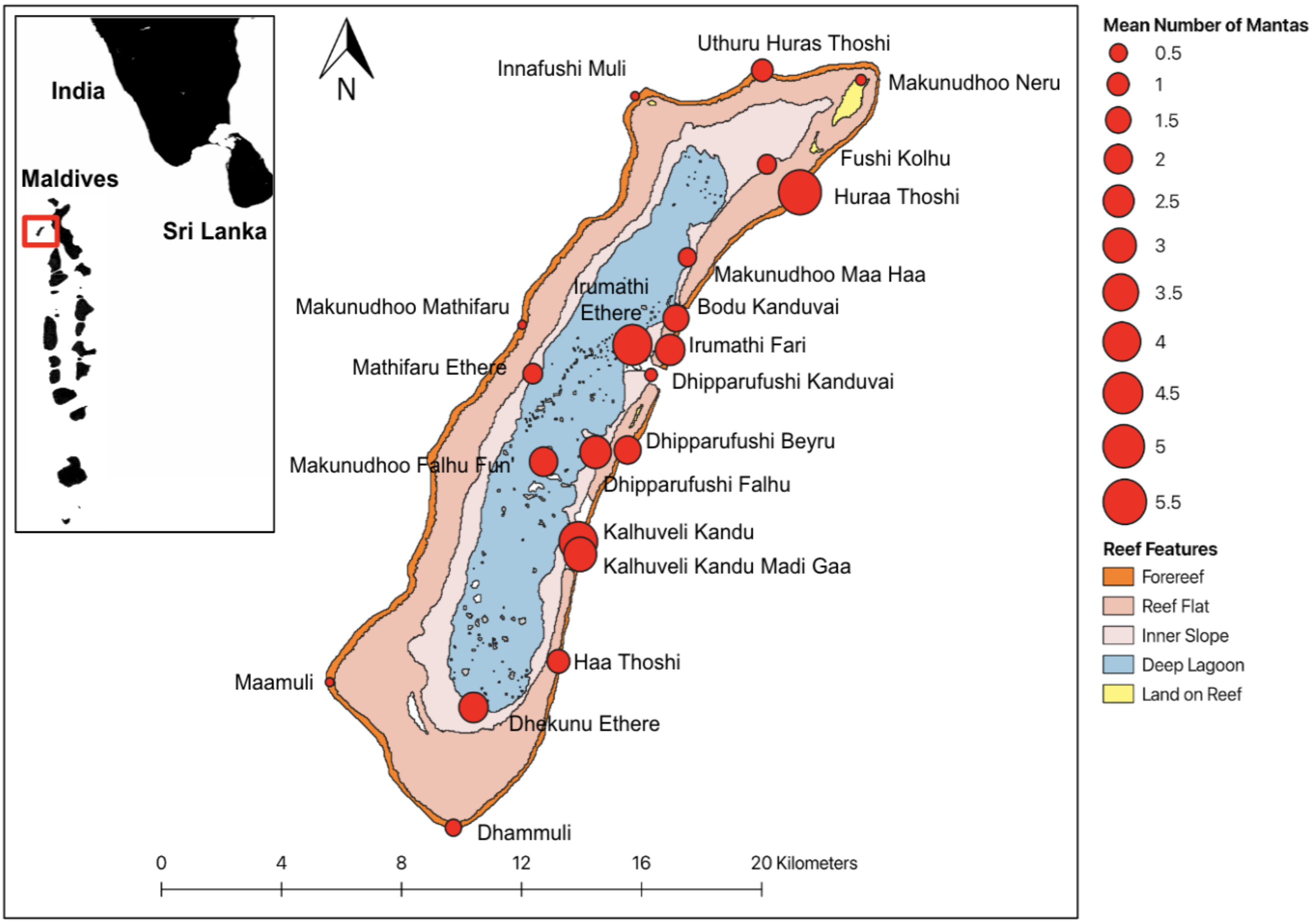

Figure 1. Mean number of *Mobula alfredi* sightings in the 21 sites surveyed in Makunudhoo. The mean number of sightings corresponds to the size of the node at each survey site. To describe bias

of uneven sampling, the approximate number of sightings at each location was divided by the respective number of surveys undertaken. Map created in QGIS 3.32.0-Lima (http://www.qgis.org) using reef features from Millennium Coral Reef Mapping Project (MCRMP) (https://data.unep-wcmc.org/datasets/1); MCRMP validated maps provided by the Institute for Marine Remote Sensing, University of South Florida (IMaRS/USF) and Institut de Recherche pour le Développement (IRD, Centre de Noume´a), with support from NASA. MCRMP unvalidated maps provided by IMaRS, USF with support from NASA and further interpreted by UNEP World Conservation Monitoring Centre (www.unep-wcmc.org). Inset top left: the Maldives Archipelago in the Central Indian Ocean with the study area highlighted in the red box.

2.2 Survey Effort

Data collection was carried out using a research vessel by trained Manta Trust researchers and interns. In the context of this study, sightings are defined by a confirmed photo-ID of an individual at a site within the Makunudhoo Atoll on a given day. Four types of surveys were undertaken: drone (n=5); remote sensing including remote underwater photo (RUP) and remote underwater video (RUV), (n=69); snorkelling (n=350); and surface observations (n=644). Remote underwater cameras were deployed for approximately 12 hours to correspond with sunrise and sunset hours where possible. Surface observations only took place in cases where individuals could not be tracked.

During a two-year study period, 1068 surveys were undertaken over 158 survey days (Table 1). Surveys were conducted at 21 different sites around the atoll (Figure 1). They occurred in March 2022 (n=375, 28 days); April 2022 (n=41, 3 days); December 2022 (n=255, 18 days); January 2023 (n=238, 17 days); and February 2023 (n=159, 13 days). The surveys were carried out during the north-east (NE) monsoon, which occurs from December to March (Anderson *et al.,* 2010; Harris *et al.,* 2020), when sighting numbers are expected to be at their highest (Charpy-Roubaud, Charpy & Larkum, 2001).

Surveys were conducted between 0600-1800 during data collection days. The number of surveys (hereby survey effort) conducted per site ranged from 2-147 (average = 51), (Table 1). Survey effort was not consistent at all sites; they were prioritised both inside and outside the eastern side of the atoll, in sites that were more accessible by boat, or where sightings were most likely to occur, which creates some sampling bias (Harris *et al.*, 2020). Weather conditions, current and tide limited accessibility to sites in certain geographical locations. As a result, sites in the far north, far south and western side of the atoll were surveyed less frequently. Some sites were also revisited more than once in one survey day which can also create bias in sighting probabilities. Variation in survey effort is a well-known limitation of photo-ID studies (Harris *et al.,* 2020) however, the dataset still provides the best evidence of *M. alfredi* presence in Makunudhoo, to date.

Table 1. Survey effort showing the number of surveys and number of repeated surveys carried out at each site during the study period. Columns showing: **a)** number of surveys carried out at each study site; **b)** number of days each site was surveyed out of the total 158 survey days; **c)** average number of hours spent surveying each site (hrs:min); **d)** number of times a survey was repeated at the same site in one survey day, not including the initial survey; **e)** number of days a survey was repeated at each site, out of the 158 total survey days; **e,i)** number of repeated surveys that reflected a different survey type; **e,ii)** number of days where surveys were repeated more than twice at the same site.

Site	Survey Effort			Repeated Surveys				Total No. of Sightings
	No. of Surveys[a]	No. of Days Surveyed[b]	No. of Hours Surveyed[c]	No. of Repeated Surveys[d]	Repeated Survey (Days)[e]	Different Survey Types[e(i)]	More than 2 surveys Repeated[e(ii)]	
Bodu Kanduvai	147	72	20:24	75	63	25	8	120
Dhammuli	5	4	5:15	1	1	0	0	0
Dhekunu Ethere	4	4	4:12	0	0	0	0	2
Dhipparufushi Beyru	61	53	4:43	8	8	5	0	60
Dhipparufushi Falhu	76	59	13:09	17	13	7	4	113
Dhipparufushi Kanduvai	85	63	5:16	22	21	3	1	2
Fushi Kolhu	43	39	23:12	4	4	1	0	15
Haa Thoshi	13	10	6:37	3	3	0	0	10
Huraa Thoshi	104	71	14:40	33	32	14	1	272
Innafushi Muli	2	2	1:10	0	0	0	0	0
Irumathi Ethere	113	69	6:06	44	34	16	7	239
Irumathi Fari	51	44	10:31	7	7	4	0	56
Kalhuveli Kandu	84	63	12:15	21	19	13	3	190
Kalhuveli Kandu Madi Gaa	99	64	20:26	35	34	33	1	179
Maamuli	3	3	2:42	0	0	0	0	0
Makunudhoo Falhu Fun'	16	13	6:35	3	3	2	0	15
Makunudhoo Maa Haa	45	39	15:17	6	6	3	0	9
Makunudhoo Mathifaru	2	2	5:45	0	0	0	0	0
Makunudhoo Neru	101	67	10:45	34	32	1	2	3
Mathifaru Ethere	12	11	12:02	1	1	1	0	3
Uthuru Huras Thoshi	2	2	1:04	0	0	0	0	1
TOTAL	**1068**							**1289**

2.3 Data Collection: Photographic Identification (photo-ID)

When *M. alfredi* were encountered, underwater digital still and video cameras were used to capture ventral side photo-ID's of individuals where possible. *Mobula alfredi* were identified using morphological characteristics (Marshall, Compagno & Bennett, 2009) including dorsal colouration, spot patterns and absence of the caudal spine (Couturier *et al.*, 2011). The images of individual inter-branchial areas captured unique marking patterns; elaborate patches, shading and gill-plate spot patterns which enabled individual identification (Deakos, 2010; Kitchen-Wheeler, 2010), (Figure S2). Photographs with clear abdominal images also provided enough information to identify the sex of the individual, determined by the presence of claspers on the pelvic fins. The size class (disc width) and state of the claspers in males were also used as a proxy for sexual maturity where possible (Kitchen-Wheeler, Ari & Edwards, 2011; Stevens, 2016).

Other data including behavioural activity of each individual was also recorded. The behavioural activities were categorised into feeding; cleaning; cruising and courtship (Harris *et al.*, 2020). Activities that dominated an encounter were considered the primary behaviour exhibited by an individual, in cases where they engaged in multiple activities. Other notable biological data was recorded when applicable to assist with individual identification, including, pregnancy, mating scars, injuries and other indications of physical condition (Kitchen-Wheeler, 2010).

The Maldives Manta Conservation Programme (MMCP) photo-ID database encompasses all the *M. alfredi* ever recorded in the Maldives since ID data collection started in 2005; 5744 individuals have been identified to date. Photographs were visually matched with the database to manage new identifications and resightings events; this was performed by two separate researchers before the inclusion of new individuals into the database.

Considering that survey duration was generally short (average = 43 minutes, SD = ± 1:40), and surveys sometimes overlapped, a time threshold was used to avoid counting duplicate sightings of individuals that have been recorded at the same site on the same day. Individuals that were identified during overlapping surveys, consecutive surveys, or occurred at the same time under a different survey type, were considered duplicates and omitted as sightings. Individuals that were resighted at the same site on the same day with a difference in survey start time of less than two hours, were also considered duplicates and subsequently omitted. Any individuals above a two-hour difference in survey start time were counted as sightings. The two-hour threshold represented a difference of morning and afternoon survey times, thus reflecting important differing temporal variables.

2.4 Data Analysis

2.4.1 Population Demographics, Habitat Use and Regional Movement

The number of sightings across the survey period and at each survey site were used to provide a descriptive analysis of population demographics, habitat use and visitation patterns of *M. alfredi* in Makunudhoo. A discovery curve was created to show the total number of individuals identified over the survey period as a function of the number of surveys conducted. The curve is expected to reach an asymptote as the number of new identifications approaches the true population of the atoll (Couturier *et al.,* 2011; Kitchen-Wheeler, Ari & Edwards, 2011).

Sightings data were used to assess the differences in habitat use by sex and maturity status. Records of behavioural activity exhibited by sightings at each survey site were also used to identify key feeding or cleaning areas. Resighting events, defined by an individual revisiting the same survey site on multiple occasions, were used to calculate site affinity and identify key habitats. Inter-atoll movement was also assessed; individuals that have been previously identified in the Maldives and therefore already exist in the MMCP photo-ID database (hereby referred to as previously documented individuals), were categorised by location of their initial sighting to reveal any movement patterns between atolls.

2.4.2 Boosted Regression Tree (BRT): Modelling Temporal Influences

Boosted regression trees (BRT) modelling was used to investigate the relationship between three predictor variables and *M. alfredi* sightings across Makunudhoo. The predictor variables defined in this study include temporal (time of day, day of the year) and moon illumination, all of which have been shown to influence *M. alfredi* presence at other locations (Andrzejaczek *et al.,* 2020). In this instance, the response variable was the approximate number of individuals observed by researchers (excluding surveys where no sightings were seen), instead of the confirmed number of individuals identified, to compensate for potential missed photo-ID's. This response variable was also used to reflect the mean number of *M. alfredi* in Figure 1.

Hour of the day corresponds to the hour of the start of a survey, and day of the year, reflects the day between 1-365 (January 1st is day 1) where a survey occurred when sightings were present. Moon illumination data showing the fraction of the moon illuminated (moon phase) was obtained from the American Navy Astronomical Applications Department (https://aa.usno.navy.mil/data/MoonFraction).

BRT is a model averaging technique based on two algorithms which include regression trees and boosting (Elith & Leathwick, 2017). It is an advantageous technique that improves predictive performance, due to its ability to model interactions between response variables and fit complex non-linear relationships whilst accounting for complex interactions between predictors (Elith, Leathwick & Hastie, 2008). Specifications of various parameters are required to build the model: tree complexity *(tc)* which indicates the number of interactions that should be modelled, learning rate *(lr)*, which regulates the contribution of each tree to the model, and bag fraction *(bf)* which controls the stochasticity of a randomly selected subset of the data at each iteration (Elith, Leathwick & Hastie, 2008; Harris & Stevens, 2021).

The BRT was conducted using R v. 4.2.2 (R Core Team, 2022). The model was fitted with the Gaussian distribution using the gbm.step() function of the dismo R package (Harris & Stevens, 2021; Hijmans *et al.,* 2017). Trees were built with the following model parameters: *tc* of 3, *lr* of 0.005 and *bf* of 0.9 (Elith, Leathwick & Hastie, 2008; Harris & Stevens, 2021). Other combinations of these parameters were also tested but did not improve model performance (Table S1).

To quantify how well the model fit with the data, the pseudo determination coefficient percentage of deviance explained (D^2) was calculated using the following form (Harris & Stevens, 2021; Nieto & Mélin, 2017): D^2 = 1 – (residual deviance / total deviance). The results suggest the relative level of influence of the predictor variables (Elith & Leathwick, 2017). This is calculated by finding the average number of times each predictor variable is chosen for splitting and the squared improvement of these splits. This result is scaled to 100 across all variables, and the variable with the highest numbers reflects a larger influence on the response variable (Elith, Leathwick & Hastie, 2008). Partial dependency plots were generated using the Dismo R package. The outputs show the relative influence of predictor variables after considering the mean influence of each predictor variable (Hastie, Tibshirani & Friedman, 2009). Statistical scripts were used from GitHub (https://github.com/JBjouffray/ggBRT), (Jouffray, 2019) to create pairwise interaction plots and visually assess the collinearity between predictor variables.

3. Results

3.1 Population Demographics, Habitat Use & Regional Movement

A total of 1289 sightings (2022, n=706; 2023, n=583) were recorded at 17 of the 21 sites surveyed in Makunudhoo across the study period (Table 2). From these, 323 *M. alfredi* were identified, including 141 (43.7%) females, 165 (51.1%) males and 17 (5.3%) unsexed individuals. Of this total, 240 (74.3%) individuals were classified as new to the database and the remaining 83 (25.7%) were resightings of previously documented individuals.

Table 2. *Mobula alfredi* sightings data at 21 survey sites in Makunudhoo Atoll during the study. Columns showing: **a)** Latitude and longitude of each site given in decimal degrees; **b)** number of surveys at each site reflecting survey effort; **c)** approximate number of *Mobula alfredi* observed by researchers; **d)** mean number of sightings per survey (calculated using the number of sightings at a site/number of surveys undertaken at respective site, to correct for survey effort); **e)** total number of individuals that visited each site. * Denotes key aggregation areas (>100 sightings per site).

Site Name	Latitude[(a)]	Longitude[(a)]	No. of Surveys[(b)]	Approx No. of Mantas[(c)]	Sightings	Mean No. of Sightings per Survey[(d)]	Total Individuals[(e)]
Bodu Kanduvai*	6.347392	72.653133	147	242	120	0.8	85
Dhammuli	6.200669	72.586117	5	2	0	0	0
Dhekunu Ethere	6.235311	72.592178	4	9	2	0.5	2
Dhipparufushi Beyru	6.309456	72.638553	61	112	60	1.0	55
Dhipparufushi Falhu*	6.308847	72.628917	76	203	113	1.5	90
Dhipparufushi Kanduvai	6.331111	72.645622	85	10	2	0	2
Fushi Kolhu	6.391753	72.680519	43	29	15	0.3	14
Haa Thoshi	6.248583	72.61775	13	15	10	0.8	10
Huraa Thoshi*	6.383708	72.690442	104	582	272	2.6	134
Innafushi Muli	6.411417	72.640808	2	0	0	0	0
Irumathi Ethere*	6.339753	72.640019	113	505	239	2.1	141
Irumathi Fari	6.338297	72.651347	51	120	56	1.1	54
Kalhuveli Kandu*	6.283039	72.623711	84	362	190	2.3	115
Kalhuveli Kandu Madi Gaa*	6.279406	72.624278	99	298	179	1.8	110
Maamuli	6.242592	72.548856	3	0	0	0	0
Makunudhoo Falhu Fun'	6.306086	72.613239	16	33	15	0.9	14
Makunudhoo Maa Haa	6.364964	72.656553	45	26	9	0.2	9
Makunudhoo Mathifaru	6.345508	72.606872	2	0	0	0	0

Makunudhoo Neru	6.416069	72.708831	101	4	3	0	3
Mathifaru Ethere	6.331461	72.610036	12	9	3	0.3	2
Uthuru Huras Thoshi	6.418811	72.679119	2	2	1	0.5	1
TOTAL			1068	2563	1289		841

Overall, 1113 sightings occurred at six key aggregation sites (>100 sightings per site). Findings were analysed in the context of the number of sightings per site which may be influenced by survey effort. Huraa Thoshi and Irumathi Ethere had the highest number of sightings (n>200), followed by Kalhuveli Kandu (Table 2). The same pattern of abundance was revealed with approximate number of sightings. However, Kalhuveli Kandu revealed the second highest mean number of sightings (Figure 2), which contrasts these abundance patterns, suggesting a larger number of individuals were sighted per survey compared to Irumathi Ethere. The low survey effort at Uthuru Huras Thoshi, Dhekunu Ethere and Mathifaru Ethere was reflected in their below average sighting numbers (<61). Dhipparufushi Kanduvai (n=2) and Makunudhoo Neru (n=3) also demonstrated low sighting numbers, but maintained an above average survey effort (>51), indicating sightings are not as common in these areas.

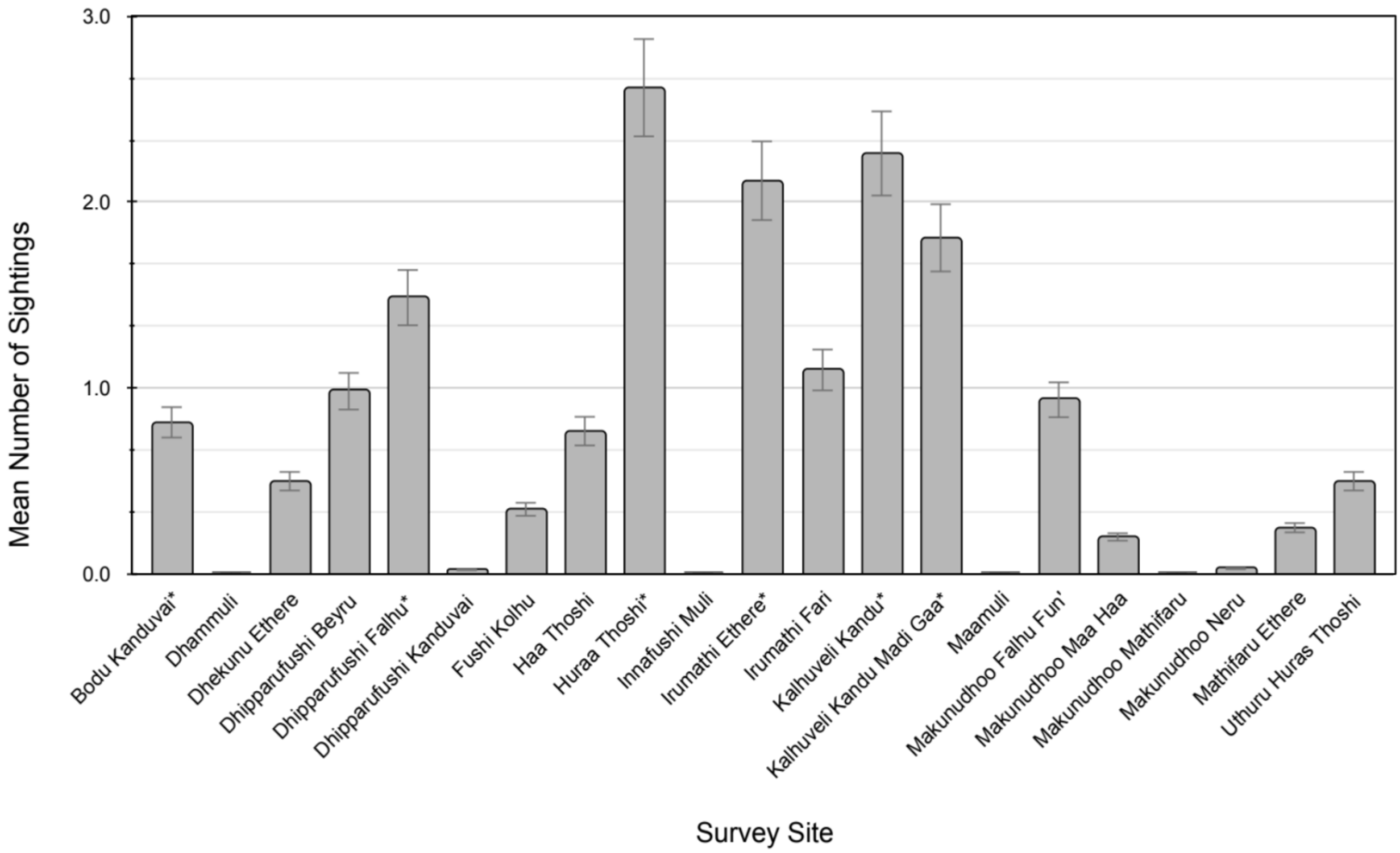

Figure 2. Mean number of *Mobula alfredi* sightings per survey site. To correct for survey effort, the number of sightings at each location was divided by the number of surveys conducted at the respective site. Error bars denote the standard deviation of each mean value. * Denotes key aggregation areas identified in the study.

3.1.1 Discovery Curve

The discovery curve shows a steady rate of newly identified *M. alfredi* in Makunudhoo across the survey period (Figure 3). New individuals were identified in 138 (12.9%) surveys of the total 1068 surveys conducted. The curve did not reach an asymptote which indicates that the entire *M. alfredi* subpopulation in Makunudhoo was not identified. This suggests that the subpopulation may exceed the 323 individuals currently known, and new individuals are yet to be discovered.

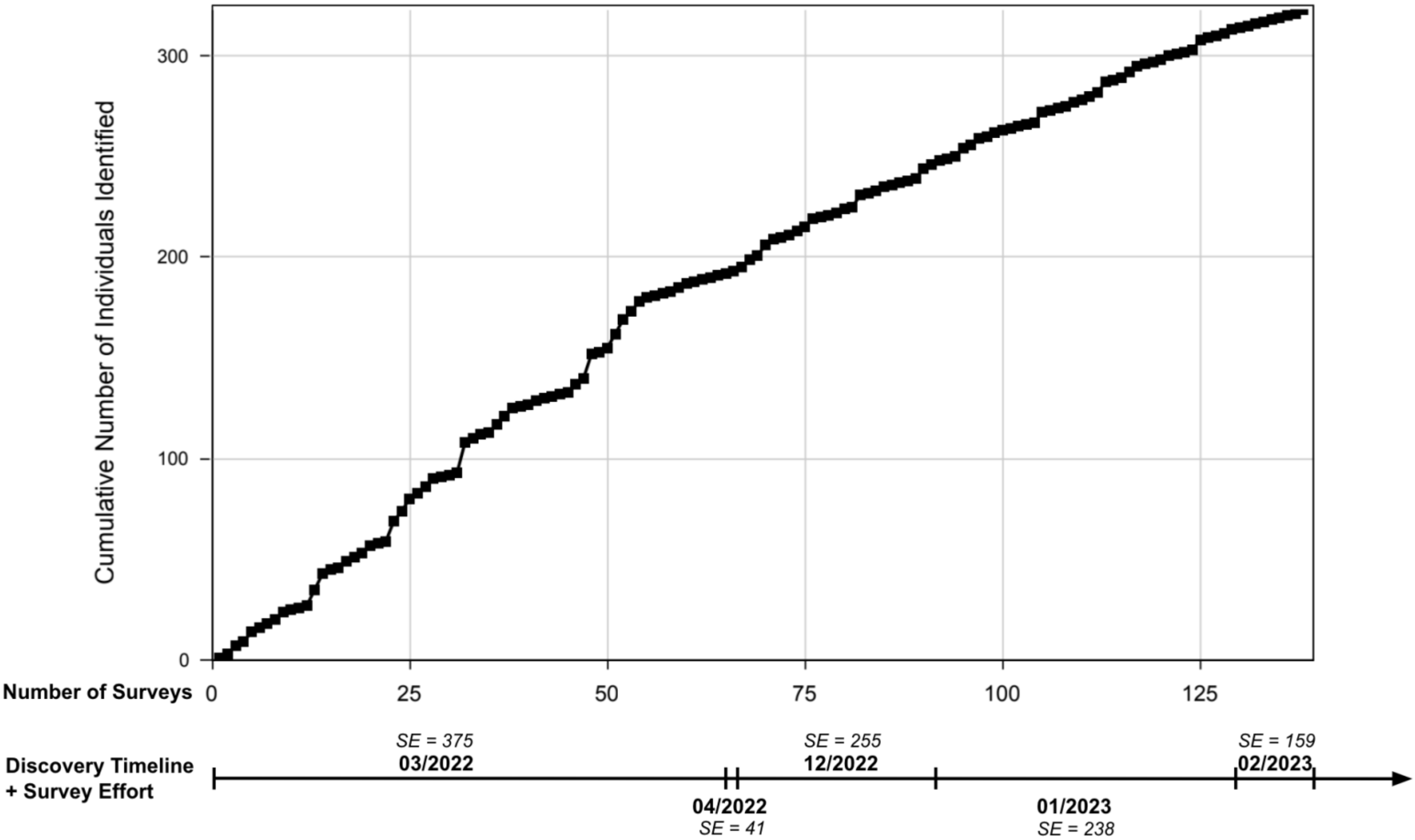

Figure 3. Discovery curve for the cumulative number of new individual *Mobula alfredi* sighted in 17 sites in Makunudhoo. Newly identified individuals (recruitment) are reported per survey in each site in chronological order and over the total five month study period (March 2022, April 2022, December 2022, January 2023, February 2023).

3.1.2 Sex & Maturity

The subpopulation shows a fairly equal sex ratio where 165 males and 141 females represented the total known population (Table 3). The sex of 17 individuals could not be identified in cases where photographs of genitalia were either absent or could not be confidently assessed. Huraa Thoshi demonstrated the highest number of female visitors (n=65), whereas the highest number of male visits were made to Irumathi Ethere (n=71) and Huraa Thoshi (n=68). Most sites were more biassed to male visits, which can be explained by the higher abundance of males present in this subpopulation.

Table 3. Number of male and female *Mobula alfredi* sightings and individuals identified at each survey site during the study period.

Site Name	Sightings				Individuals			
	Male	Female	Unsexed	Total Sightings	Males	Females	Unsexed / Unknown	Total Individuals
Bodu Kanduvai	57	58	5	120	45	38	2	85
Dhekunu Ethere	0	2	0	2	0	2	0	2
Dhipparufushi Beyru	40	17	3	60	36	16	3	55
Dhipparufushi Falhu	52	56	5	113	40	46	4	90
Dhipparufushi Kanduvai	0	2	0	2	0	2	0	2
Fushi Kolhu	7	7	1	15	7	6	1	14
Haa Thoshi	5	5	0	10	5	5	0	10
Huraa Thoshi	141	128	3	272	68	65	1	134
Irumathi Ethere	118	110	11	239	71	62	8	141
Irumathi Fari	26	28	2	56	26	26	2	54
Kalhuveli Kandu	93	96	1	190	66	48	1	115
Kalhuveli Kandu Madi Gaa	90	86	3	179	60	47	3	110
Makunudhoo Falhu Fun'	4	10	1	15	4	9	1	14
Makunudhoo Maa Haa	5	4	0	9	5	4	0	9
Makunudhoo Neru	1	2	0	3	1	2	0	3
Mathifaru Ethere	3	0	0	3	2	0	0	2
Uthuru Huras Thoshi	0	0	1	1	0	0	1	1
TOTAL	**642**	**611**	**45**	**1289**	**165**	**141**	**17**	**323**

Of the 323 individuals in the subpopulation, 39.7% (n=125) were juveniles, 15.5% (n=50) were subadults and 35.6% (n=115) were adults (Figure 4)**.** Adult males (n=86, 26.6%) and juvenile females (n=94, 29.1%) made up the largest proportion of the subpopulation whereas female subadults (n=2, 0.6%) and juvenile males (n=31, 9.6%) made up the smallest. The high proportion of female juveniles (>68% of sightings) were sighted at Huraa Thoshi (n=99), Irumathi Ethere (n=76), Kalhuveli Kandu (n=66) and Kalhuveli Kandu Madi Gaa (n=66); similar patterns were found for adult male sightings (Table 4). These numbers reflect sites with greater survey effort and should therefore be interpreted with caution.

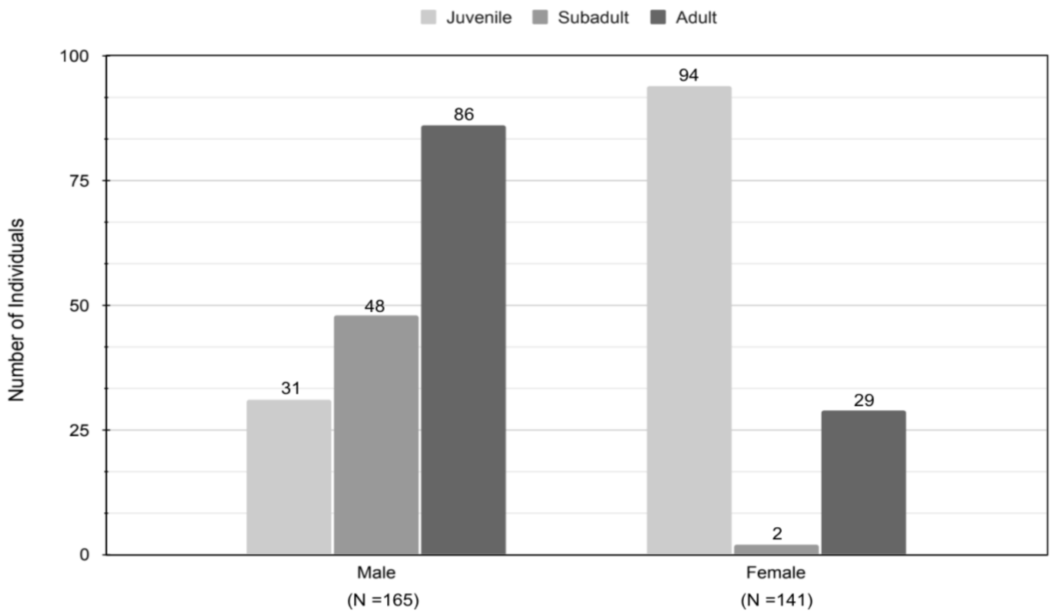

Figure 4. Sex and maturity status of individual *Mobula alfredi* identified in the Makunudhoo subpopulation. Numbers across the top indicate the total number of individuals pertaining to each demographic category; number of individuals where sex is unknown was not accounted for (n=17).

Table 4. Summary of all sightings at every survey site, categorised by demographic group (sex & maturity status). Table does not account for the number of sightings where sex (n=36) or female maturity status (n=49) is unknown.

Site Name	Female Juvenile	Female Subadult	Female Adult	Male Juvenile	Male Subadult	Male Adult	Total No. of Sightings
Bodu Kanduvai	44		10	12	13	32	120
Dhekunu Ethere	1						2
Dhipparufushi Beyru	15		2	9	12	19	60
Dhipparufushi Falhu	35		14	8	10	34	113
Dhipparufushi Kanduvai	2						2
Fushi Kolhu	6		1	4	2	1	15
Haa Thoshi	4		1	2	1	2	10
Huraa Thoshi	99	6	18	28	35	78	272
Irumathi Ethere	76		21	15	28	75	239
Irumathi Fari	21		5	3	7	16	56
Kalhuveli Kandu	63	3	19	20	38	35	190
Kalhuveli Kandu Madi Gaa	63	3	15	13	34	43	179
Makunudhoo Falhu Fun'	7		2	1	1	2	15
Makunudhoo Maa Haa	3	1		2	3		9
Makunudhoo Neru	1		1	1			3
Mathifaru Ethere				2	1		3
TOTAL	**440**	**13**	**109**	**120**	**185**	**337**	

3.1.3 Habitat Use

A total of 13 sites were identified as feeding areas, considering *M. alfredi* sightings (>100) were predominantly engaged in feeding (Figure 5). Other activities recorded by the remaining sightings consisted mostly of cleaning (13.9% of sightings) followed by cruising (4.8% of sightings). Courtship behaviour was only recorded by 0.5% of all sightings and was thus considered negligible for this study.

The largest proportion of sightings that engaged in feeding behaviour were found at Huraa Thoshi and Irumathi Ethere. Huraa Thoshi is situated in the fore reef (furthest away from shore) in the north-eastern corner of the atoll, whereas Irumathi Ethere is located around reef flats, inside the protected lagoons, central to the atoll (Figure 1); other important feeding areas were located in channels. Kalhuveli Kandu Madi Gaa was classified as the only cleaning station, where 93% (n=167) of sightings were primarily exhibiting cleaning behaviour (Figure 5).

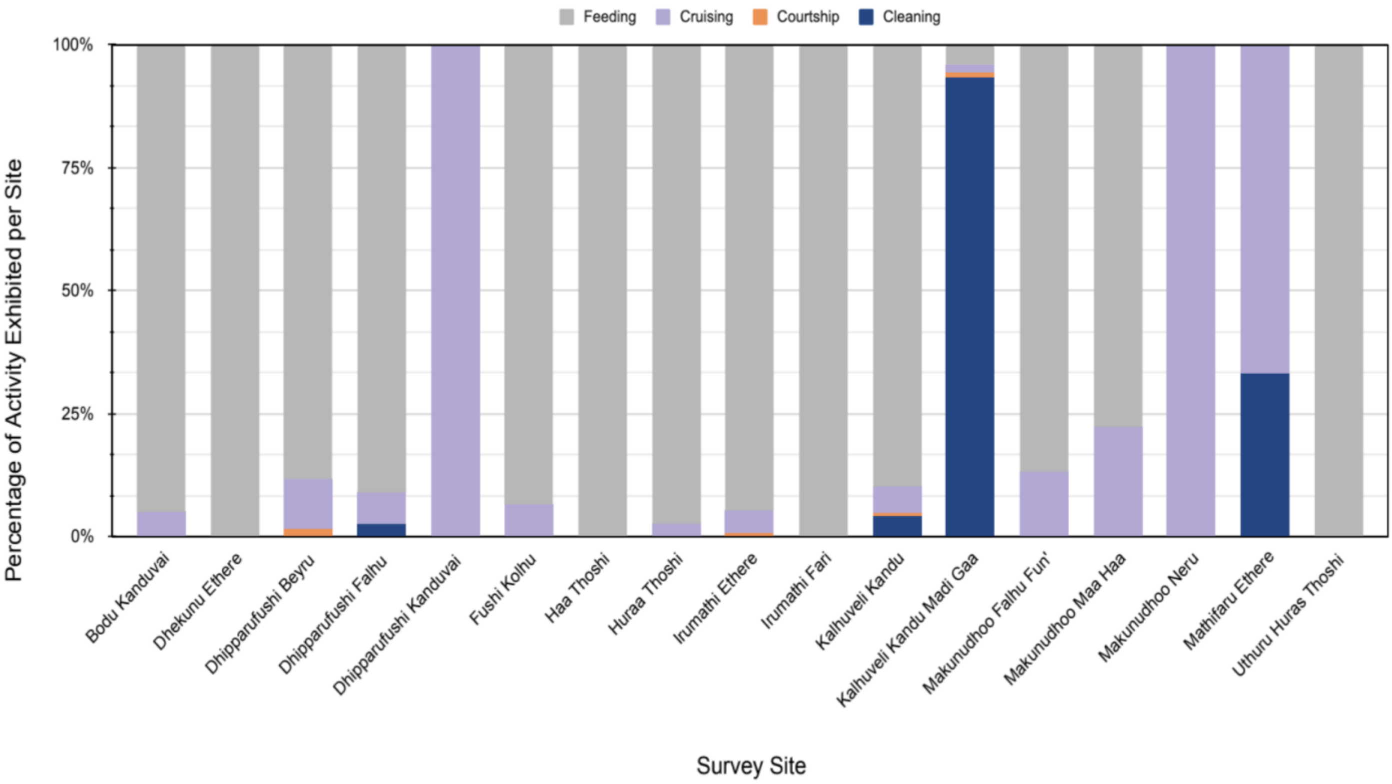

Figure 5. Breakdown of the primary behaviour exhibited by *Mobula alfredi* sightings at each survey site during the study period. A comparison of the percentages of each activity includes feeding (grey), cruising (purple), courtship (orange) and cleaning (blue). Not accounting for one sighting where two primary behaviours were recorded.

3.1.4 Site Affinity

Of the 323 individuals identified in this study, 251 (77.7%) were resighted between 1-16 times, with an average of 4.8 (SD± 2.7) resightings per individual. The remaining individuals in the subpopulation (n=72) were only sighted once during the study. Resighting events by the same individual were recorded at 11 of the 17 survey sites where sightings occurred. During the study, individuals were resighted in up to six different locations after their initial sighting (Figure 6). Only 6% (n=15) of individuals were exclusively found resighting to the same location from which they were initially recorded. The majority (>60%) of individuals were resighted at either one or two different locations from their initial sighting.

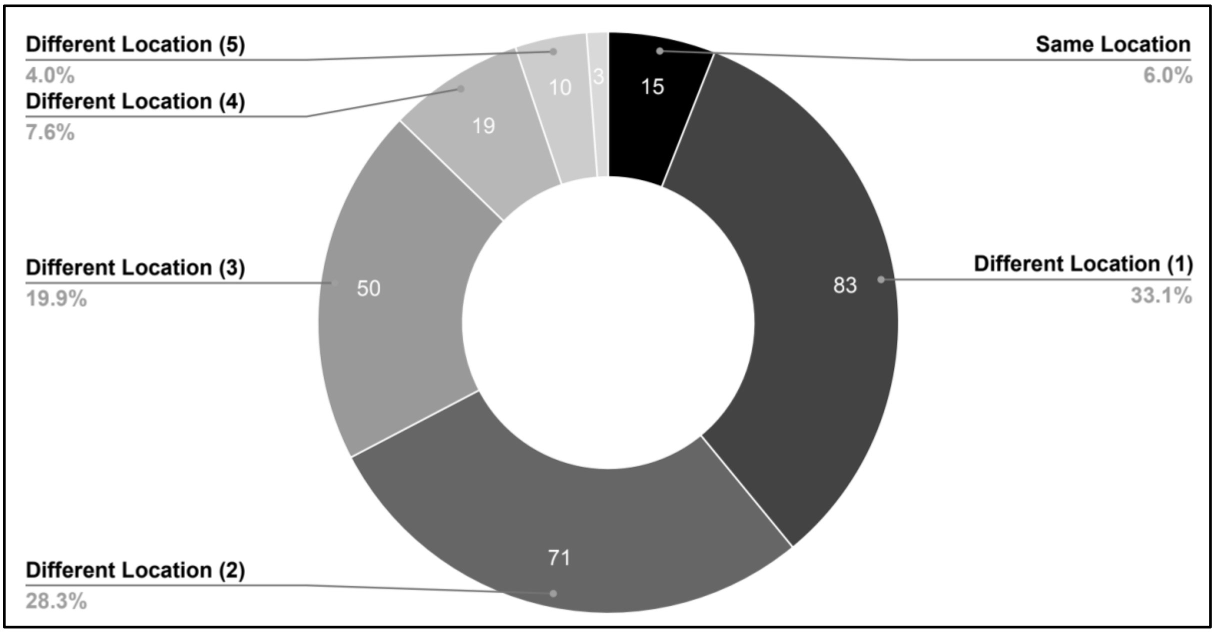

Figure 6. The percentage of individual *Mobula alfredi* resightings (n=251) that occurred either exclusively at the same survey site, or up to six different survey sites within Makunudhoo during the study period.

A total of 243 individual *M. alfredi* were resighted at the same site from which they were initially identified, resighting between one and eight times (Table 5); the majority (n=137, 56.4%) resighted only once. Huraa Thoshi, Kalhuveli Kandu and Kalhuveli Kandu Madi Gaa experienced the highest number of resightings per individual; five individuals resighted to either of these locations between seven and eight times. It is important to note that Dhipparufushi Kanduvai (SE=85) and Makunudhoo Neru (SE=101) did not have any resighting events, despite having an above average survey effort (>51).

Table 5. The number of times *Mobula alfredi* resighted to the same site in Makunudhoo during the study period. Percentages calculated using the ID column, which describes the total number of individuals that visited each respective survey site.

Site Name	ID	Number of Resighting Events								No. of Resightings per Site
		1st	2nd	3rd	4th	5th	6th	7th	8th	
Bodu Kanduvai	85	14 (16.5%)	6 (7.1%)	3 (3.5%)						35
Dhipparufushi Beyru	55	5 (9.1%)								5
Dhipparufushi Falhu	90	16 (17.8%)	2 (2.2%)	1 (1.1%)						23
Fushi Kolhu	14	1 (7.1%)								1
Huraa Thoshi	134	27 (20.1%)	17 (12.7%)	9 (6.7%)	2 (1.5%)	4 (3.0%)	1 (0.7%)	1 (0.7%)	1 (0.7%)	137
Irumathi Ethere	141	30 (21.3%)	14 (9.9%)	6 (4.3%)	3 (2.1%)	2 (1.4%)				98
Irumathi Fari	54	2 (3.7%)								2
Kalhuveli Kandu	115	23 (20.0%)	3 (2.6%)	10 (8.7%)	2 (1.7%)			1 (0.9%)		74
Kalhuveli Kandu Madi Gaa	110	17 (15.5%)	11 (10.0%)	4 (3.6%)	1 (0.9%)			2 (1.8%)		69
Makunudhoo Falhu Fun'	14	1 (7.1%)								1
Mathifaru Ethere	2	1 (50%)								0
TOTAL		**137**	**53**	**33**	**8**	**6**	**1**	**4**	**1**	**445**

3.1.5 Tracking Inter-atoll Movements

A total of 83 individuals from the 323 individuals described in this study, were previously documented in the MMCP photo-ID database. Initial sightings of these individuals occurred in 10 different northern atolls in the Maldives archipelago; no initial sightings occurred in southern atolls (Figure 7)**.** Only two previously documented individuals were initially sighted in Makunudhoo, and these sightings only occurred recently in 2021. The majority (≥ 20) of initial identifications were made in Baa Atoll (n=41, distance ≈ 134 km) and in Thiladhunmathi Atoll (n=20; distance ≈ 85 km); the majority (n=28) of individuals were first sighted in Hanifaru Bay, Baa Atoll. The furthest location by which previously documented individuals were initially sighted was Kalhahandhi Huraa, Ari Atoll (distance ≈ 280 km), whereas the closest distance was in Gaakoshinbi Faru, Thiladhunmathi Atoll (≈ 40 km).

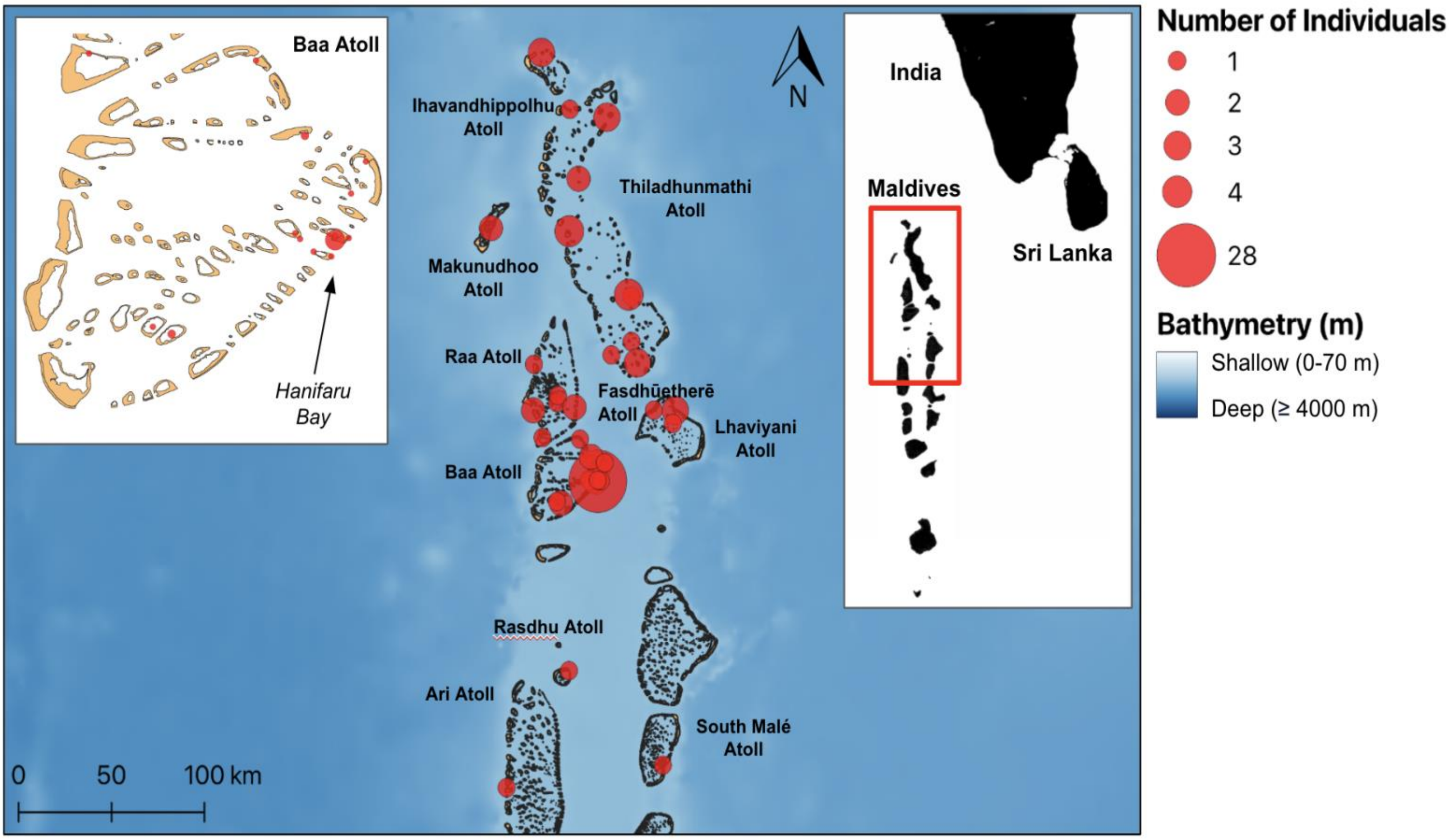

Figure 7. Original sighting location (labelled by atoll) of previously documented *Mobula alfredi* (n=83). The number of individuals corresponds to the size of the node at each location and is described per site, per atoll. Map created in QGIS 3.32.0-Lima (http://www.qgis.org) using bathymetry from GEBCO Bathymetric Compilation Group (2023) GEBCO 2023 Type Identifier (TID) Grid (doi:10.5285/f98b053b-0cbc-6c23-e053-6c86abc0af7b) and reef features from Millennium Coral Reef Mapping Project (MCRMP) (https://data.unep-wcmc.org/datasets/1); MCRMP validated maps provided by the Institute for Marine Remote Sensing, University of South Florida (IMaRS/USF) and Institut de Recherche pour le De´veloppement (IRD, Centre de Noume´a), with support from NASA. MCRMP unvalidated maps provided by IMaRS, USF with support from NASA and further interpreted by UNEP World Conservation Monitoring Centre (www.unep-wcmc.org). Inset top left: close-up of initial sightings in Baa Atoll; arrow pointing to Hanifaru Bay where the majority (n=28) of initial sightings were made. Inset top right: the Maldives Archipelago in the Central Indian Ocean; general area where all previously documented individuals were first sighted, highlighted in red box.

3.2 Boosted Regression Tree (BRT): Modelling Temporal Influences

The estimated D^2 suggests that 15% of the overall deviance was explained by the model. Partial dependency plots (Figure 8) indicate that day of the year (63.2%) was the most accurate predictor of sightings probabilities, followed by hour of the day (28.8%) and moon illumination (8%).

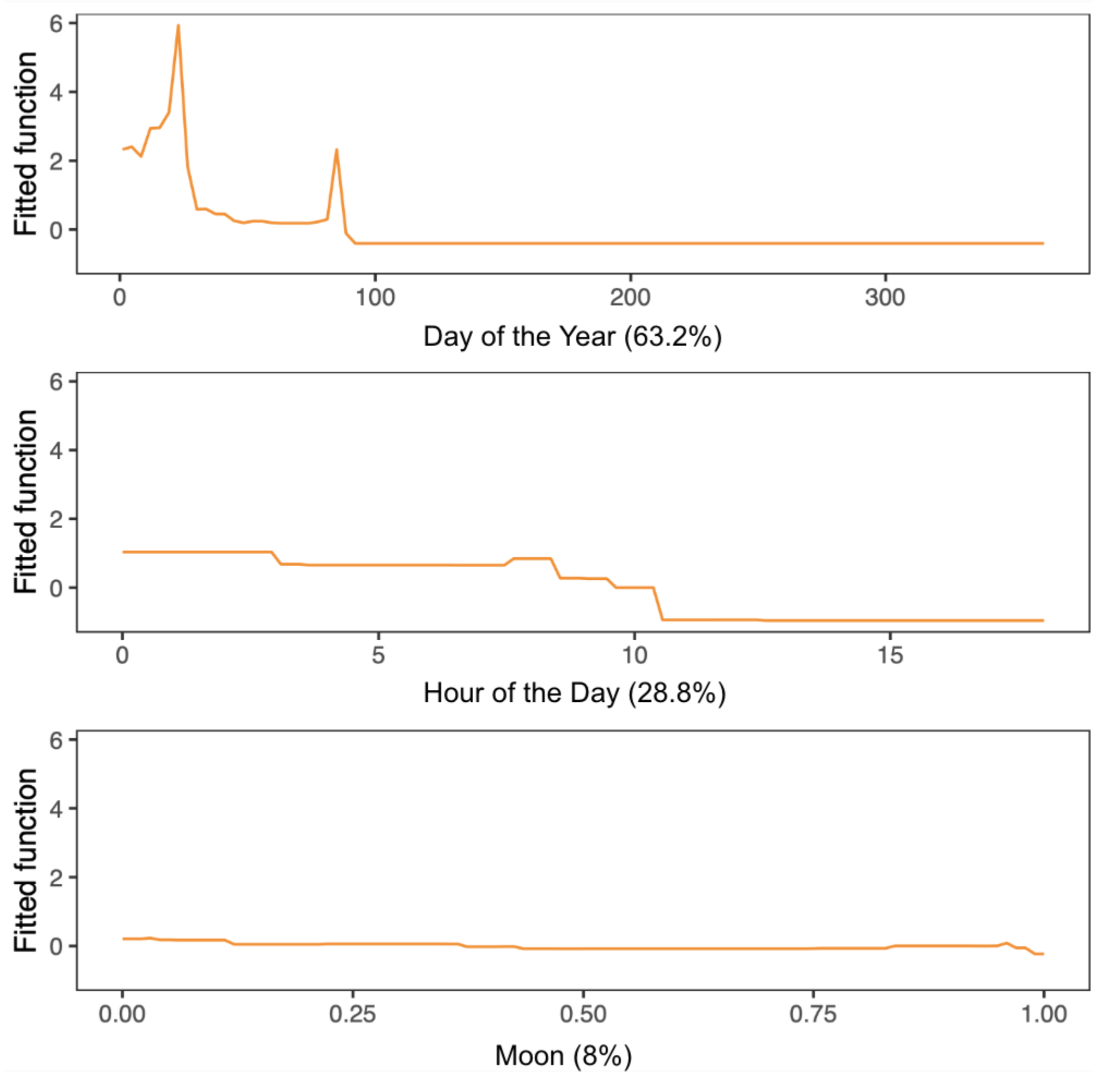

Figure 8. Partial dependency plots showing the effect of each predictor variable: day of the year, hour of the day and moon illumination on the occurrence of *Mobula alfredi* at Makunudhoo over the study period. The orange line shows smooth partial decency.

Partial dependency plots indicated that the probability of sightings increased depending on the day of the year (63.2%). The probability of sightings, only considering the months surveyed in this study (December-April), peaked between day 20-40, which represents late January to early February. Sightings probability reached a smaller peak between day 80-90, representing mid to late March. Sighting probability was also influenced by the hour of the day (28.8%), which was confined to 0600-1800 reflecting the time frame where data was collected; sighting probability peaked around 0800. Moon illumination had close to no influence on sighting probability (8%), and thus considered negligible for this study.

The strongest interactions occurred between day of the year and hour of the day (Figure 9; Table S2). Here, the probability of sightings were consistently highest in the morning, between 0600-1100 throughout all the months represented during the survey period. More specifically, sighting probability was highest between 0600-1000 within the first 10 days of the year (January), and then again between days 60-80 (beginning of March). The probability of sightings occurring in the morning decreases later in the season. These interactions should not be considered in isolation as they may be influenced by other variables or survey effort.

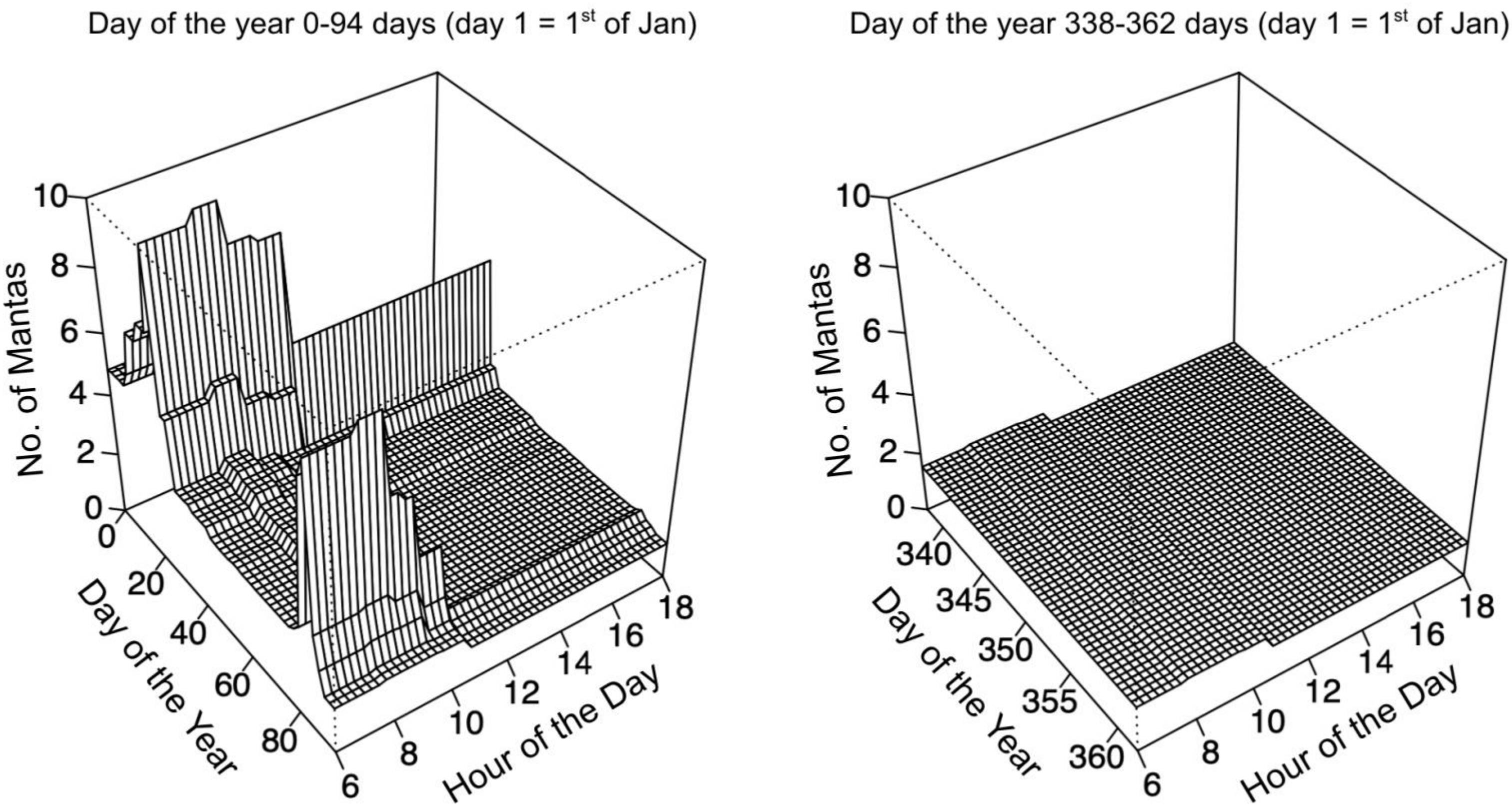

Figure 9. Pairwise interactions between predictor variables showing the probability of *Mobula alfredi* sightings (z axis) in Makunudhoo. The X axis represents the day of the year, where day 1 is the 1st of January. Y axis represents the hour of the day, ranging between hours 0600-1800, reflecting the time period where surveys were conducted. Left plot: represents day 0-94 which is January 1st to April 4th. Right plot: represents day 338-362 which is December 4th to December 28th.

4. Discussion

This study provides the first ever photo-ID record of *M. alfredi* in Makunudhoo Atoll, providing empirical evidence of their movement, habitat use by demographic and key aggregation areas. The study identified 323 individuals, frequenting 17 sites around the atoll. The majority (74%) of individuals were new identifications which suggests that a new subpopulation has been described.

4.1 Population Demographics

Variations in visitation patterns of *M. alfredi* have previously been associated with differences in habitat use by sex and maturity status (Peel *et al.,* 2019; Stevens, 2016). Here, photo-ID data showed juvenile females and adult males constituted the majority (56%) of the subpopulation, representing most sightings at key feeding and cleaning areas.

The large presence of adult male sightings in Makunudhoo may be attributed to predator avoidance (Germanov *et al.,* 2019; Stevens, 2016). For example, males reach a smaller maximum disc width compared to females. Their size difference can make them more susceptible to predatory attack which means they seek more sheltered habitats, such as shallow reefs (Marshall *et al.,* 2011). More intensive use of aggregation areas by males may also be associated with mate-seeking behaviour where they move more frequently between sites in search for females, and thus have a greater chance of being sighted (Germanov *et al.,* 2019).

Juvenile *M. alfredi* have also been found to reside in shallow reef habitats (i.e. lagoons), in larger numbers and over longer periods of time compared to adults (Pate & Marshall, 2020; Setyawan *et al.,* 2020; Stevens, 2016). Lagoons have been suggested to be important nursery grounds, providing many benefits to juveniles such as reliable food availability (Germanov *et al.,* 2019; McCauley *et al.,* 2014). Juveniles may therefore be relying on the consistent opportunities of shallow water foraging available in the study area. For example, Makunudhoo has a singular lagoon which is created by a perimeter of forereef. The semi-enclosed nature of the atoll, combined with its proximity to deep water, mostly likely draws plankton into the shallow lagoon via access through channels (Germanov *et al.,* 2019). Lagoons may also act as important refuges from large offshore predators and provide opportunities to thermoregulate after deep foraging dives (McCauley *et al.,* 2014; Stevens, 2016). The steady recruitment of new juveniles in this study provides strong evidence that these aggregation sites are important nursery areas, particularly for feeding, which are frequented following birth (Germanov *et* *al.,* 2019). However, the sexual bias towards females in the juvenile population is ambiguous. The variation in sex ratios present in different habitats, which has been exhibited by many species of elasmobranchs, is poorly understood (Marshall *et al.,* 2011). Ultimately, the abundance of juveniles may also suggest proximity to a breeding or birthing ground, which is an area worthy of further investigation (Marshall, Dudgeon & Bennett, 2011).

4.1.1 Implications for Management

Establishing MPAs with no-take fishing zones, exclusion zones, outboard engine restrictions (Carpentier *et al.*, 2019) or vessel number limits would greatly reduce potential for direct injury (Strike *et al.,* 2022). This is especially important in Makunudhoo where there is a limited capacity for boat travel. Makunudhoo has a small number of channels that give access to the inside of the lagoon, all of which are located on the eastern side of the atoll. Survey effort was concentrated on this side due to better accessibility by boat; movement to the western side of the atoll was limited by distance, tide or lack of channels. The accessibility of boat passageways suggests an increase in tourism pressure has the potential to concentrate marine traffic in areas that overlap with juvenile aggregations.

4.2 Visitation Patterns: Habitat Use & Regional Movement

This study identified six key aggregation areas; five of which were used primarily for feeding and one of which was designated as a cleaning station. A high number of sightings at these locations, would suggest that they are important areas of habitat use. In this study, all aggregation areas were located on the eastern side of the atoll, which can be explained by lack of survey effort on the western side of the atoll. However, considering Makunudhoo's westwardly location in comparison to other atolls, movements of *M. alfredi* to this area are considered consistent with seasonal migration patterns, where individuals follow productivity in the west during the NE monsoon (Anderson *et al.,* 2011; Harris *et al.,* 2020; Kitchen-Wheeler, Ari & Edwards, 2011). Here, results are confined to observations made over the NE monsoon period, which suggests most of the visitation patterns of and between aggregation areas identified in this study are most likely linked to these monsoonal migrations.

4.2.1 Site Affinity

A proportion (85% of resightings) of *M. alfredi* displayed site affinity (> 50 resightings) to three key feeding areas and the existing cleaning station. Site affinity was used to describe this behaviour as it is unknown whether resighting events might be transient visitations of more broad-scale movements across the archipelago. Data was collected over a short time period which makes it unclear whether sightings were exhibiting true site fidelity (Couturier *et al.,* 2011).

Various levels of site affinity were recorded, where 78% of the subpopulation resighted between 1-8 times. Approximately 31% of resightings accounted for one revisit to the same location. Only 12 individuals displayed high site affinity (5-8 resighting events), which occurred at Huraa Thoshi and Irumathi Ethere, two popular feeding areas. The variation in site affinity among individuals suggest they are partial migrators where some individuals remain resident and others migrate to their preferred areas, which could be influenced by their demographic and associated needs (Andrzejaczek *et al.,* 2020). However, it is also important to note that the variation in resighting patterns may also be influenced by survey effort (Sequiera *et al.,* 2019).

Site affinities have been well-documented in *M.alfredi* populations (Dewar *et al.,* 2008; Jaine *et al.,* 2014; McCauley *et al.,* 2014). Factors that may explain this behaviour include species' reliance on habitats for foraging (Couturier *et al.,* 2018) refuge (Stevens, 2016), reproduction (Marshall, Dudgeon & Bennett, 2010) and opportunities to clean or socialise (Harris *et al.,* 2021; Perryman *et al.,* 2019). Cleaning and feeding were the most common activities to occur at all sites that were routinely encountered in Makunudhoo (Kitchen-Wheeler, 2010), suggesting the most likely driver associated with site affinity is foraging and cleaning opportunities (Armstrong *et al.,* 2016; Couturier *et al.,* 2011). Considering the demographic bias present in this subpopulation, the association between variations in site visitation by sex or maturity status is less clear.

4.2.2 Inter-atoll Movement

Initial sightings of previously documented individuals revealed that the furthest distance travelled from surrounding atolls was 280 km, which is consistent with other studies documenting up to 241 km of distance travelled between atolls (Andrzejaczek *et al.,* 2020). Initial sightings were also exclusively located in northern atolls, suggesting broad-scale inter-atoll movement may be limited by distance and give evidence to the fragmentation of subpopulations (Harris & Stevens, 2021). It is likely that these individuals travelled to Makunudhoo as part of the seasonal migration considering its western location in comparison to where they were originally sighted (Jaine *et al.,* 2012).

4.2.3 Implications for Management

The majority (n=28) of previously documented individuals were first sighted in Hanifaru bay, Baa Atoll (≈ 138 km away) which is recognised as an important feeding area for *M. alfredi,* particularly during the SW Monsoon (Harris *et al.,* 2020; Harris & Stevens, 2021; Stevens, 2016). This provides quantitative evidence of connectivity between Baa and Makunudhoo Atoll. Locating and quantifying these long-distance movements is important to help inform legislation so that popular migration corridors are protected against vessel traffic via MPAs and exclusion zones. This in turn can ensure safe passage and accessibility between sites that are relied on at different times of the year (Andrzejaczek *et al.,* 2020; Harris & Stevens, 2021). MPAs should therefore not be confined to individual sites but instead cover larger areas, accounting for the network of aggregations that cover the sub population's range, especially important because of their highly mobile nature (Peel *et al.,* 2019; Stevens & Froman, 2018). Protecting larger areas of reef from human stressors also gives potential to improve reef resilience at larger scales (Folke *et al.,* 2004).

4.3 Temporal Influences on *M. alfredi* Presence

The BRT provided evidence that sightings were most likely to peak in January and between 0600-1000. Similar observations were made by Andrzejaczek *et al.,* (2020), where *M. alfredi* were detected mostly in December and January. Various acoustic telemetry studies have revealed diel visitation patterns suggesting *M. alfredi* detections in shallow, coastal reef systems are generally made during daylight hours, a behavioural pattern which has become typical of this species (Couturier *et al.,* 2018; Dewar *et al.,* 2008; Harris *et al.,* 2021; Peel *et al.,* 2019). These patterns have been associated with foraging strategies where *M. alfredi* follow the vertical migrations of reef-associated zooplankton which accumulate in shallow reefs during the day (Alldredge & King, 2009; Harris & Stevens, 2021). Understanding temporal occurrence has important implications for MPA management. For example, zoning and activity restrictions could be implemented during distinct times of the year when *M. alfredi* sightings are expected to be at their highest (Germanov *et al.,* 2019).

4.4 Recommendations for *M. alfredi* Conservation

Comprehensive management plans are crucial for MPA's to offer adequate protection. Venables *et al.,* (2016) suggests comprehensive management plans should operate under the precautionary principle. This approach helps guide management intervention by protecting both people and the environment from anthropogenic stressors, in cases where the magnitude of tourism impacts are inconclusive. A precautionary approach is particularly relevant to Makunudhoo considering tourism development is in its infancy. Physical and behavioural changes of *M. alfredi* in response to high tourism interaction have already been recorded in the Maldives. This approach will help prevent activities known to disturb this species, until more is known about the subpopulation and their habitat use throughout the atoll (Harris *et al.,* 2020; Venables *et al.,* 2016).

The Ningaloo Marine Park in Western Australia is an example of a well developed management programme that operates under the precautionary principle, resulting in an ecologically sustainable whale shark interaction industry (Harris *et al.,* 2020; Venables *et al.,* 2016). They have adopted several on-site enforcement regulations, which based on its success in terms of compliance, could also be applied to *M. alfredi* interaction tourism. For example, operators require specific licences to conduct interaction tours, helping to control time limits with and distances to individuals, boat speeds, and number of passengers permitted on vessels. Licensing systems helped to monitor and control industry growth by regulating the extent of interactions and associated tourism pressures (Venables *et al.,* 2016). Licensed operators are also required to help in data collection, by submitting photo-ID's and recording supplementary information including number of passengers, GPS coordinates during interactions, perceived size and sex of individuals and their direction of travel (DPAW, 2013). Allowing operators to assist in industry data collection can help create a sense of ownership, and in turn, initiate more commitment to the MPA (Iacarella *et al.,* 2021). In Makunudhoo, this approach would help gather more long-term data and enhance the understanding of the current patterns revealed in this study (Mau & Wilson, 2008).

4.5 Study Limitations and Future Research

The current study is subject to limitations. In particular, the variation of survey effort expended at each site meant that habitat use and population demographics were only representative of sites where more surveys were undertaken (Guttridge *et al.,* 2009). This limits the potential to identify more key aggregation areas that likely exist throughout the atoll. To further the current study, future research should prioritise more photo-ID studies to improve subpopulation size estimates and to substantiate the revealed demographic bias and suggested patterns of habitat use. These data can provide a good baseline for future studies aiming to quantify the effect of tourism expansion (Harris *et al.*, 2020). Future research would also benefit from satellite tagging to monitor long-term movement patterns and site use, per demographic group (Stewart *et al.,* 2018).

Conclusions

This study used photo-ID records and Boosted Regression Tree modelling to develop a baseline understanding of the *M. alfredi* subpopulation in Makunudhoo. Population demographics and patterns of habitat use suggest this region is an important nursery area. As the *M. alfredi* tourism industry will continue to expand, comprehensive, species-specific MPA management should be focused on areas where juveniles naturally aggregate, using spatial and temporal patterns of habitat use revealed in this study, to ensure long-term survivorship of this vulnerable species.

[Word Count: 5942]

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Supporting Information

Supplementary Information: Figure S1

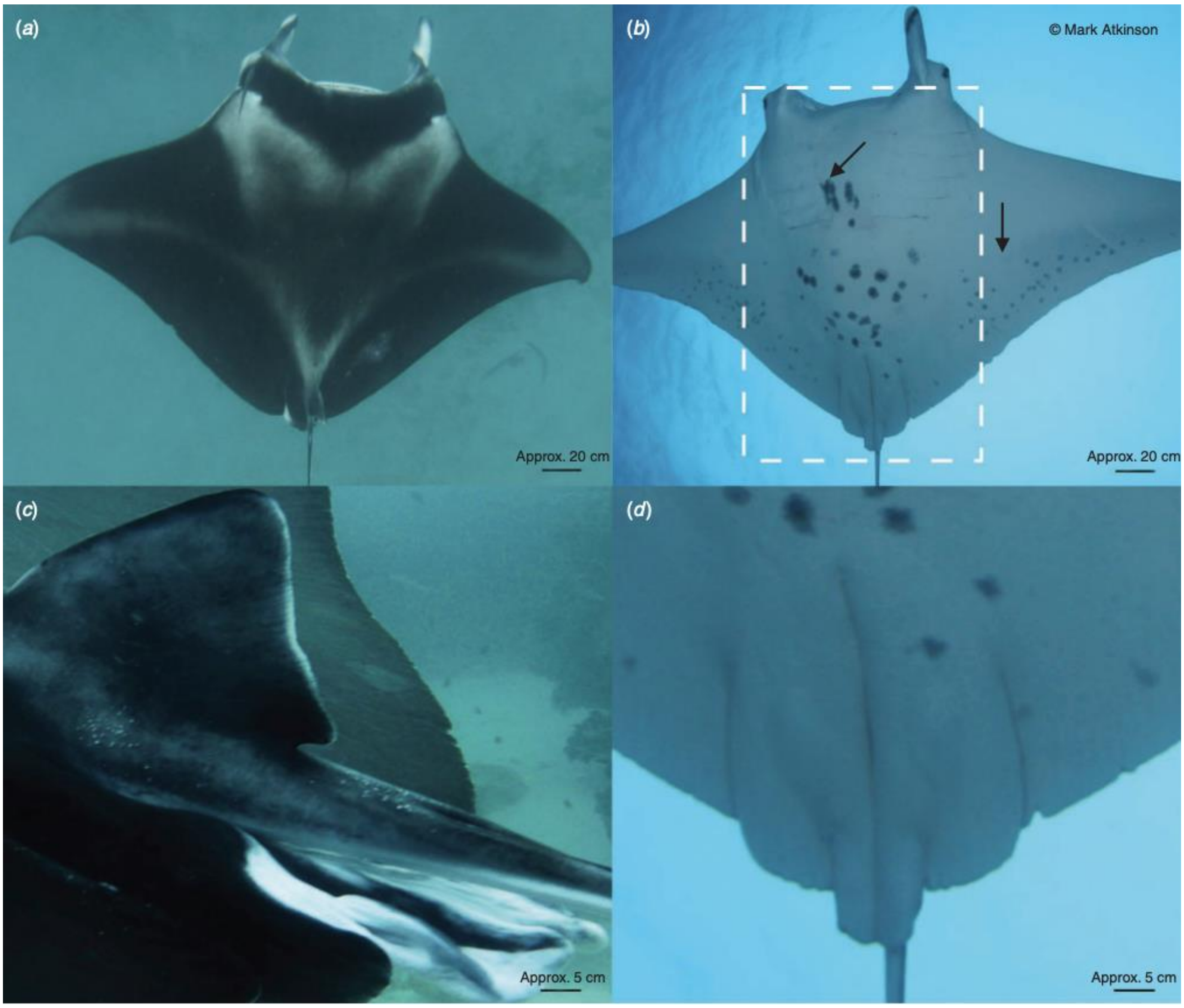
Figure S1. Environmental Protection Agency (EPA): Protected Area List - 15th June 2023. Download available from: https://en.epa.gov.mv/publications.

	Designation	Type	Atoll	X	Y	Declaration Date	Directives
1	Makunudhoo Kandu Olhi	MPA	K	73.38333	4.566667	1-Oct-95	E/95/32
2	Rasfari Region	Island/MPA	K	73.35091	4.395907	1-Oct-95	E/95/32
3	Banana Reef (Gaathu Giri)	MPA	K	73.53187	4.23933	1-Oct-95	E/95/32
4	Giravaru Kuda Haa	MPA	K	73.41592	4.216615	1-Oct-95	E/95/32
5	Lions Head (Dhekunu Thilafalhuge Miyaruvani)	MPA	K	73.426	4.178928	1-Oct-95	E/95/32
6	Hans Hass Place (Gulhi Falhu)	MPA	K	73.46681	4.172309	5-May-20	(IUL)438-/ENV/438/2020/102
7	Emboodhoo Kanduolhi	MPA	K	73.53005	4.0859	1-Oct-95	E/95/32
8	Guraidhoo Kanduolhi	MPA	K	73.46729	3.894478	3-Sep-20	(IUL)438-/ENV/438/2020/150
9	Mayaa Thila	MPA	AA	72.85335	4.082949	1-Oct-95	E/95/32
10	Orimas Thila Region	MPA	AA	72.95097	3.9816	1-Oct-95	E/95/32
11	Fish Head (Mushimasmigili Thila)	MPA	AA	72.91652	3.936948	1-Oct-95	E/95/32
12	Kudarah Thila	MPA	AA	72.9196	3.561571	1-Oct-95	E/95/32
13	Fushifaru Region	MPA	Lh	73.51667	5.483333	1-Oct-95	E/95/32
14	Miyaru Kandu Region (Dhevana kandu)	MPA	V	73.50064	3.579358	1-Oct-95	E/95/32
15	Fushi kandu	MPA	Dh	72.92927	2.996712	21-Oct-99	10-C/99/38
16	Villigilee Thila	MPA	R	72.95702	5.379164	21-Oct-99	10-C/99/38
17	Kuredhu Express (Kuredhu Kanduolhi)	MPA	Lh	73.47549	5.55638	21-Oct-99	10-C/99/38
18	Nassimo Thila (Lankan Thila)	MPA	K	73.53333	4.283333	21-Oct-99	10-C/99/38
19	Karibeyru Region	MPA	AA	72.9614	4.095034	21-Oct-99	10-C/99/38
20	Rangali Kandu (Madivaru)	MPA	ADh	72.72116	3.593881	21-Oct-99	10-C/99/38
21	Vattaru	MPA	V	73.42492	3.221988	21-Oct-99	10-C/99/38
22	Lhazikuraadi (Hakuraa Thila)	MPA	M	73.5464	2.945248	21-Oct-99	10-C/99/38
23	Filitheyo Kandu	MPA	F	73.03915	3.201294	21-Oct-99	10-C/99/38
24	Dhigili Giri	MPA	B	73.04164	5.147151	5-Jun-11	138-FS2/1/2011/35
25	Eidhigali Kilhi Koattey Area	Mangrove/MPA	S	73.07795	-0.58534	13-Sep-18	2018/R-105
26	Huraa Mangrove	Mangrove	K.	73.60134	4.334108	14-Jun-06	174-AB1/2006/13
56	Naalaa Huraa (Sand Bank)	Sandbank/MPA	Sh	73.03819	6.120348	17-Jun-19	(IUL)438-ENV/438/2019/150
57	Fohdhiparu	Sandbank/MPA	N	73.20755	5.742961	17-Jun-19	(IUL)438-ENV/438/2019/150
58	Kendhikulhudhoo mangrove area	Terrestrial/MPA	N	73.41425	5.958828	17-Jun-19	(IUL)438-ENV/438/2019/150
59	Orimasthila	MPA	N	73.24996	5.845508	17-Jun-19	(IUL)438-ENV/438/2019/150
60	Bodulhaimendhoo	Island/MPA	N	73.30496	6.010009	17-Jun-19	(IUL)438-ENV/438/2019/150
61	Farikede Area	MPA	Gn	73.43769	-0.31723	22-Jul-20	(IUL)438-ENV/438/2020/129
62	Kuda Kandu Area	MPA	S	73.14012	-0.63011	3-Sep-20	(IUL)438-ENV/438/2020/162
63	Maakilhi and Feheli Kilhi	Mangrove/ Wetland	S	73.09226	-0.61283	22-Sep-20	(IUL)438-ENV/438/2020/162
64	Maafishi Kilhi	Mangrove/ Wetland	S	73.22487	-0.6086	22-Sep-20	(IUL)438-ENV/438/2020/162
65	Mathi Kilhi	Mangrove/ Wetland	S	73.23364	-0.59249	22-Sep-20	(IUL)438-ENV/438/2020/162
66	Sehlhifushi & Hiriyadhoo Region	Island/MPA	Lh	73.64205	5.417067	8-Oct-20	(IUL)438-ENV/438/2020/179
67	Vavvaru, Dhandifalhu Finolhu and Dhandifalhu Kanduolhi	Sandbank/Island	Lh	73.35242	5.409832	8-Oct-20	(IUL)438-ENV/438/2020/179
68	Dhashugiri Finolhu	Sandbank	Lh	73.42672	5.42414	8-Oct-20	(IUL)438-ENV/438/2020/179
69	Anemone Thila	MPA	Lh	73.49722	5.44194	8-Oct-20	(IUL)438-ENV/438/2020/179
70	Maakoa	Island	Lh	73.43144	5.356865	8-Oct-20	(IUL)438-ENV/438/2020/179
71	Thanburudhoo Region	Island/MPA	K	73.58419	4.314556	5-Nov-20	(IUL)438-ENV/438/2020/209
72	Gan Boda Fengandu Area	Island/MPA	L	73.53376	1.885685	23-Dec-21	(IUL)438-ENV/438/2021/371
73	Maabaidhoo Koaru and Fushi Kandu Area	Island/MPA	L	73.53068	2.039574	23-Dec-21	(IUL)438-ENV/438/2021/371
74	Bodu Finolhu and Vadinolhu Kandu Olhi Area	Sandbank/MPA	L	73.3685	2.019181	23-Dec-21	(IUL)438-ENV/438/2021/371
75	Gaadhoo Turtle Nesting, Mangrove and Seagrass Area	Island/MPA	L	73.44555	1.821906	23-Dec-21	(IUL)438-ENV/438/2021/371
76	Gaadhoo - Hithadhoo Kandu Area	MPA	L	73.43552	1.805808	23-Dec-21	(IUL)438-ENV/438/2021/371
77	Hithadhoo Wetland and Surrounding Marine Area	Wetland/MPA	L	73.3855	1.792731	23-Dec-21	(IUL)438-ENV/438/2021/371
78	Kaashidhoo Wetland Area	Wetland	K	73.46898	4.959003	13-Feb-21	(IUL)438-ENV/438/2021/24
79	Maldives Victory Wreck	MPA	K	73.52566	4.179256	13-Feb-21	(IUL)438-ENV/438/2021/24

27	Hurasdhoo	Island/MPA	ADh	72.77467	3.666983	14-Jun-06	174-AB1/2006/13
28	Olhugiri	Island/MPA	B	72.90589	5.00154	14-Jun-06	174-AB1/2006/13
29	Hithaadhoo Island	Island/MPA	GA	73.24232	0.849573	14-Jun-06	174-AB1/2006/13
30	South Ari Atoll MPA	MPA	ADh	72.79942	3.454913	11-Jul-19	(IUL)438-ENV/438/2019/175
31	Hanifaru Area	MPA	B	73.14384	5.17388	5-Jun-06 & 5-Jun-11	138-EE/2009/19 & 138-FS2/1/2011/35
32	Angafaru Area	MPA	B	73.08859	5.188966	5-Jun-09	138-EE/2009/19
33	Mendhoo Region	Island/MPA	B	72.99541	5.175546	5-Jun-11	138-FS2/1/2011/35
34	Goidhoo Koaru	Mangrove	B	72.99846	4.879428	5-Jun-11	138-FS2/1/2011/35
35	Bathalaa Region	Island/MPA	B	73.07259	5.361869	5-Jun-11	138-FS2/1/2011/35
36	Mathifaru Huraa	Island/MPA	B	72.89361	4.813333	5-Jun-11	138-FS2/1/2011/35
37	The wreck of "Corbin"	MPA	B	72.90083	4.909167	5-Jun-11	138-FS2/1/2011/35
38	Maahuruvalhi Reef Region	MPA	B	72.86032	5.186928	5-Jun-11	138-FS2/1/2011/35
39	Bandaara Kilhi and Surrounding Wetlands	Mangrove/Wetland	Gn	73.43063	-0.29959	13-Sep-18	2018/R-106
40	Dhandimagu kilhi	Mangrove/	Gn	73.41771	-0.28562	13-Sep-18	2018/R-106
41	Thoondi Area (Fuvahmulah)	Terrestrial	Gn	73.41637	-0.27653	13-Sep-18	2018/R-106
42	Kandihera-Maakandu Channel (Addu Manta Point)	MPA	S	73.15527	-0.60963	13-Sep-18	2018/R-105
43	British Loyalty Shipwreck	MPA	S	73.11379	-0.63888	13-Sep-18	2018/R-105
44	Rasdhoo Madivaru Area	MPA	AA	72.99807	4.264382	7-Oct-18	(IUL)438-ENV/438/2018/262
45	Dhigulaabadhoo	Island	GDh	73.15431	0.213965	7-Oct-18	(IUL)438-ENV/438/2018/262
46	Farukolhu	Island	Sh	73.29859	6.19064	7-Oct-18	(IUL)438-ENV/438/2018/262
47	Baarah Mangrove Area	Terrestrial	HA	73.21189	6.814087	30-Dec-18	(IUL)438-ENV/438/2018/322
48	Keylakunu	Terrestrial	HDh	73.00937	6.603193	30-Dec-18	(IUL)438-ENV/438/2018/322
49	Neykurendhoo Mangrove Area	Terrestrial	HDh	72.98563	6.542357	30-Dec-18	(IUL)438-ENV/438/2018/322
50	Bileydhoo Thila (including Innafinolhu)	Island/MPA	HA	72.81635	7.05445	17-Jun-19	(IUL)438-ENV/438/2019/150
51	Gallandhoo	Island/MPA	HA	72.97359	6.951933	17-Jun-19	(IUL)438-ENV/438/2019/150
52	Kelaa Mangrove Area	Terrestrial	HA	73.21612	6.943761	17-Jun-19	(IUL)438-ENV/438/2019/150
53	Finey Thila	MPA	HDh	73.05934	6.744661	17-Jun-19	(IUL)438-ENV/438/2019/150
54	Innafushi	Island/MPA	HDh	72.63721	6.418002	17-Jun-19	(IUL)438-ENV/438/2019/150
55	Bollissafaru	Sandbank/MPA	Sh	73.11641	6.003466	17-Jun-19	(IUL)438-ENV/438/2019/150

Supplementary Information: Figure S2

Figure S2. Key features used to identify and sex *Manta alfredi* using **(a)** the dorsal surface coloration and **(b)** the ventral surface spot distribution (box shows the main region used for photo-identification, arrows show the spots distribution of the inter-branchial and the pectoral fin margin regions distinctive for M. alfredi), **(c)** absence of caudal spine and **(d)** presence of claspers. Taken from: Couturier *et al.,* 2011.



Supplementary Information: Table S1

Table S1. Calibration results table of the different model parameters tested. Model parameters used in this study are highlighted in yellow (Model 27).

Model	tc	lr	bf	Residual Deviance	Correlation	CV-Deviance	CV Correlation	D^2
1	1	0.005	0.5	36.2685086	0.2956079	37.8316861	0.2221559	8.40
2	1	0.005	0.7	36.5408717	0.2837459	37.6323321	0.2352944	7.71
3	1	0.005	0.9	36.9181407	0.2688023	37.8148316	0.2387371	6.76
4	1	0.001	0.5	37.0307720	0.2630290	37.8324725	0.2214797	6.47
5	1	0.001	0.7	37.0786190	0.2628829	37.8647816	0.2167622	6.35
6	1	0.001	0.9	37.0211046	0.2647385	37.6988644	0.2380074	6.50
7	1	0.0005	0.5	37.3220971	0.2558949	38.0633066	0.2042756	5.74
8	1	0.0005	0.7	37.2164905	0.2598398	37.9465266	0.2140745	6.00
9	1	0.0005	0.9	37.2028743	0.2604031	37.9466052	0.2318250	6.04
10	1	0.0001	0.5	38.2491420	0.2392605	38.6872782	0.2020557	3.40
11	1	0.0001	0.7	38.3418264	0.2350624	38.7672770	0.2271683	3.16
12	1	0.0001	0.9	38.4881918	0.2243614	38.8112460	0.2129637	2.80
13	2	0.005	0.5	35.8319383	0.3250750	37.8676361	0.2356931	9.50
14	2	0.005	0.7	35.7295893	0.3299188	38.1427950	0.2078162	9.76
15	2	0.005	0.9	35.3546367	0.3431514	37.6493463	0.2371903	10.71
16	2	0.001	0.5	35.5980579	0.3298675	37.5758796	0.2478970	10.10
17	2	0.001	0.7	35.4872321	0.3356374	37.6146444	0.2380995	10.37
18	2	0.001	0.9	35.7323340	0.3319225	38.1214774	0.2020305	9.75
19	2	0.0005	0.5	35.9493772	0.3222363	37.7175468	0.2459280	9.20
20	2	0.0005	0.7	35.9949052	0.3229629	37.8703096	0.2177361	9.10
21	2	0.0005	0.9	35.8907347	0.3272641	37.9348834	0.2121163	9.35
22	2	0.0001	0.5	37.1534104	0.3035492	38.1708462	0.2348983	6.16
23	2	0.0001	0.7	37.0860346	0.3018468	38.1817706	0.2339747	6.33
24	2	0.0001	0.9	37.8231909	0.2788721	38.9283564	0.1630441	4.47
25	3	0.005	0.5	34.4047729	0.3863245	37.9725837	0.2408470	13.12
26	3	0.005	0.7	35.1495916	0.3771079	37.9875157	0.2270179	11.22
27	3	0.005	0.9	33.8310489	0.4049946	37.5877557	0.2802934	15.00
28	3	0.001	0.5	34.7364742	0.3757938	37.4734174	0.2160574	12.27
29	3	0.001	0.7	33.9129606	0.4004109	37.3117443	0.2534493	14.34
30	3	0.001	0.9	34.1417451	0.3997095	38.0688307	0.2382682	13.77
31	3	0.0005	0.5	35.3081671	0.3683313	38.1534980	0.2066112	10.82
32	3	0.0005	0.7	34.7620957	0.3866179	37.7977312	0.2188681	12.20
33	3	0.0005	0.9	34.3746242	0.3959481	37.8867768	0.2351210	13.18
34	3	0.0001	0.5	36.2432476	0.3564053	38.1349608	0.2514415	8.46
35	3	0.0001	0.7	35.8286856	0.3689409	37.8677549	0.2455757	9.51
36	3	0.0001	0.9	37.2319264	0.3323805	38.7312459	0.1901635	5.97

Supplementary Information: Table S2

Table S2. Pairwise interactions between predictor variables. Higher values indicate a stronger interaction effect; near zero indicates negligible interactions.

Predictor 1	Predictor 2	Interaction Size
Day of the Year	Hour of the Day	390.01
Day of the Year	Moon	66.11
Hour of the Day	Moon	0.24