

Ontogenetic variation in patterns of sightings of reef manta rays in the Maldives: environmental influences, distribution, and implications for protected area management

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In collaboration with Manta Trust



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i. Declaration

I hereby certify that this dissertation, which is approximately 9,282 words in length, has been composed by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a degree. The project was conducted by me at the University of St Andrews from September 2020 to August 2021 towards fulfilment of the requirements of the University of St Andrews for the degree of Master of Science under the supervision of Dr. Sonja Heinrich and Dr. Sophie Smout.

Date: 16 August 2021

Signature: 

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iii. Abstract

Reef manta rays (*Mobula alfredi*) in the Maldives play an important role in the large tourism sector but are vulnerable to anthropogenic threats such as boat strike, fisheries bycatch, and unsustainable tourism. Increasing pressure on the marine environment and a global commitment to protect 30% of national waters by 2030 have spurred the government to expand their network of marine protected areas (MPAs), prioritising the protection of vulnerable and valuable species. Reef manta rays are late to mature and slow to reproduce, making juvenile survival critical to overall population health. This study used sightings of adult, juvenile, and young of year (YoY) reef manta rays collected at known manta ray sites throughout the Maldives from 1987 through 2019. Generalised additive models were used to identify important environmental predictors of the daily number of sightings of manta rays in each demographic group and to visually assess distribution in the heavily touristed central and north-central regions. Sightings of adult and juvenile reef manta rays were influenced by similar environmental predictors; however, chlorophyll-a and sea surface temperature were significant only for adults, and a sighting was more likely to be a juvenile than an adult in lagoonal reefs. Most sightings of YoY were estimated in lagoonal reefs, at lower concentrations of chlorophyll-a, and higher sea surface temperatures, which is consistent with shark and ray species that utilise nursery areas. Here we show that manta ray sightings are driven by a trade-off between food availability and predator avoidance, and the relative importance of lagoons to juveniles and YoY indicate that these groups prioritise predator avoidance. Focussing MPA expansion on sites with most estimated sightings per demographic group will conserve the species throughout its life. A particular focus on the protection of lagoonal reefs will enhance population health by enabling juveniles to mature and reproduce.

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1.0 Introduction

Charismatic, flagship, and umbrella species have been used globally to drive marine conservation efforts, often through the creation of marine protected areas (MPAs); MPAs ultimately provide protection to both the focal species and its associated habitat, and can aid in climate change adaptation (Zacharias and Roff, 2001; Weng *et al.*, 2015; Roberts *et al.*, 2017; Osgood *et al.*, 2020). Many flagship species are also large animals, or megafauna, that move across wide geographic extents, shifting their ranges during different times of their lives and utilising separate habitats for different behavioural activities. MPAs focussed on protecting megafauna at certain life stages or within areas of high importance for certain behaviours have been shown to provide positive benefits to the species of interest, decreasing the frequency of exposure to threats and reducing cumulative stress on the animals (Hooker and Gerber, 2004; Hooker *et al.*, 2011).

The Maldives archipelago is a chain of 26 geographic atolls in the central Indian Ocean and it contains approximately 3% of the world's reefs (Stevens and Froman, 2018). The Maldives currently has a network of 50 MPAs, however, individual MPAs are small in size (EPA, 2019). With <1% of reef area currently covered by MPA legislation and as members of the Global Ocean Alliance, which aims to protect 30% of global oceans by 2030, the Maldivian government plans to identify further key marine ecosystems to designate as marine protected areas (DEFRA; MEE, 2015; Stevens and Froman, 2018). The conservation of the marine environment is of economic importance as the nation's beaches and underwater beauty are cited as the primary motivation for tourist visits, and the tourism sector provides the largest contribution to the Maldivian GDP (approximately 30%) (MEE, 2016).

The Maldives is home to the world's largest recorded population of reef manta rays (*Mobula alfredi*) along with a more elusive and less studied population of oceanic manta rays (*M. birostris*) (Kitchen-Wheeler *et al.*, 2011; Stevens, 2016; Harris *et al.*, 2020). These charismatic animals play an important role in the Maldives' tourism industry, generating an estimated US\$8.1 million annually through snorkelling and diving trips, with an estimated annual direct economic impact of approximately US\$15.5 million (Anderson *et al.*, 2010; O'Malley *et al.*, 2013). As the Maldives looks to expand its MPA network, targeting future MPA

designation to sites important for manta rays will not only help conserve these vulnerable and valuable animals but will also help to protect the ecosystems upon which manta rays rely.

This study will focus on reef manta rays, which are listed on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species as Vulnerable to extinction (Marshall *et al.*, 2019). Globally, targeted fisheries driven by the demand for dried mobulid gill plates in Asian markets are the primary threat to reef manta ray populations, with fishing bycatch, tourism, vessel strikes, and pollution serving as additional lethal and sub-lethal threats (Couturier *et al.*, 2012; Croll *et al.*, 2016; O'Malley *et al.*, 2017; Stewart, Jaine, *et al.*, 2018). Although targeted fishing of all ray species has been outlawed in Maldivian waters since 2014, reef manta rays remain threatened by fishing bycatch, unregulated tourism, habitat degradation, and climate change (Stevens and Froman, 2018). The species' conservative life history, including slow growth, late maturity (11 years for males and 15 years for females), and low reproductive rates (reproductive periodicity of 7.9 years), make populations particularly vulnerable, with manta rays having one of the lowest rates of population growth amongst the elasmobranchs (sharks and rays) (Dulvy *et al.*, 2014; Stevens, 2016).

Manta rays, like many other elasmobranch species are thought to display ontogenetic niche shifts, with animals changing habitats at different life stages, aiming to minimise mortality and maximise growth, and, once mature, reproduce successfully (Grubbs, 2010). Mortality and growth are affected by features of habitat including food availability, predation pressure, environmental conditions, and intraspecific competition, however, intraspecific competition has not been observed in manta rays (Grubbs, 2010). Juvenile elasmobranchs tend to utilise habitats closer to shore than adults, and within the Mobulidae family, juveniles of *M. thurstoni*, *M. japanica*, *M. munkiana*, *M. alfredi*, and *M. birostris* have been observed segregated from adults, with sightings of juvenile individuals often occurring in lagoonal or shallow coastal habitats (Notarbartolo-Di-Sciara, 1988; Grubbs, 2010; Deakos *et al.*, 2011; Stewart, Jaine, *et al.*, 2018; Stewart, Nuttall, *et al.*, 2018).

For late maturing and long lived species, juvenile survival is critical to the overall health of the population due to a positive correlation between time spent in the juvenile stage and its relative importance to population survival (Heppell *et al.*, 2000; Frisk *et al.*, 2005). Juvenile

survival to adulthood is highlighted as being particularly important for exploited or threatened elasmobranch species (Frisk *et al.*, 2005). As reef manta rays spend a large portion of their lives in the juvenile stage, a better understanding of key juvenile habitat will allow for better protective measures that can positively influence overall population health (Stewart, Jaine, *et al.*, 2018).

Past research in the Maldives has identified seasonal changes in the distribution of reef manta rays throughout the archipelago, tying seasonal movement to oceanographic conditions driven by the seasonally reversing South Asian monsoon winds and the associated patterns of water movement in and around the Maldivian archipelago (Anderson *et al.*, 2011; Harris *et al.*, 2020). During the Northeast (NE) monsoon season (December – March), the predominant current flow is from east to west and during the Southwest (SW) monsoon season (May–October), the predominant current flow is from west to east; however, wind and current conditions are less predictable during the transitional months of April and November (Anderson *et al.*, 2011; Stevens and Froman, 2018). The north-south positioning of the Maldivian atoll chain and the east-west water movement across the archipelago result in higher chlorophyll-a concentrations and enhanced primary productivity on the down-current side of the atolls which, in turn, supports large quantities of zooplankton (Anderson *et al.*, 2011). Seasonal migrations allow manta rays to feed in areas of high zooplankton concentration, with the SW monsoon wind speeds and chlorophyll-a concentrations most strongly influencing reef manta ray sightings at sites on the down-current atoll edges (Anderson *et al.*, 2011; Kitchen-Wheeler *et al.*, 2011; Harris *et al.*, 2020). Reef manta rays have also been shown to visit cleaning stations on the down-current side of the atolls, where they rely upon cleaner wrasse (*Labroides spp.*) to rid them of parasites (Kitchen-Wheeler, 2010; O’Shea *et al.*, 2010; Stevens, 2016; Harris *et al.*, 2020; Stevens *et al.*, 2020).

A better understanding of environmental characteristics that influence site use by reef manta rays in the Maldives will allow for more effective protection of this vulnerable species, particularly ensuring that protected areas conserve manta rays during the vulnerable juvenile stage of their lives, allowing them to mature and reproduce and helping to ensure population vitality. This study aims to elucidate ontogenetic variation in habitat use and distribution of reef

manta rays in the Maldives to highlight priority areas for protection by: (1) determining the environmental influences on sightings of adult, juvenile, and young of year (YoY) reef manta rays at known manta ray aggregation sites, (2) identifying key sites across the Maldivian archipelago where the number of reef manta ray sightings are greatest for each ontogenetic stage, and (3) mapping estimated reef manta ray sightings per ontogenetic stage.

2.0 Materials and Methods

2.1 Study Site

The Maldives archipelago is made up of 26 geographic atolls in the central Indian Ocean. The 870 km long archipelago is located 475 km south of India, from approximately 7 degrees North to 0.5 degrees South. The atolls form a double chain in the central Maldives with a maximum width of 128 km, but the northern and southern reaches of the country are formed by a single atoll chain. The approximately 300 km² of land area make up less than 1% of the 916,000 km² national exclusive economic zone (EEZ). Malé City is home to 38% of the population of 402,071 and, as of the most recent census, Malé and Ari Atolls saw the largest percent increases in population size (NBS, 2015). Approximately 80% of tourist bed capacity (32,176 beds) comes from the central atolls of Raa, Baa, Lhaviyani, North and South Malé, and Ari Atolls (Ministry of Tourism, 2019).

2.2 Data Collection (Manta Rays)

Data were collected between 2005 and 2019 by staff and volunteers of the Manta Trust's Maldives Manta Conservation Programme (MMCP) and opportunistically between 1987 and 2019 by citizen scientists. Surveys were performed at 294 sites in 21 atolls, with most surveys conducted at known manta ray aggregation sites during times when sightings were expected to be most likely to occur (Figure 1).

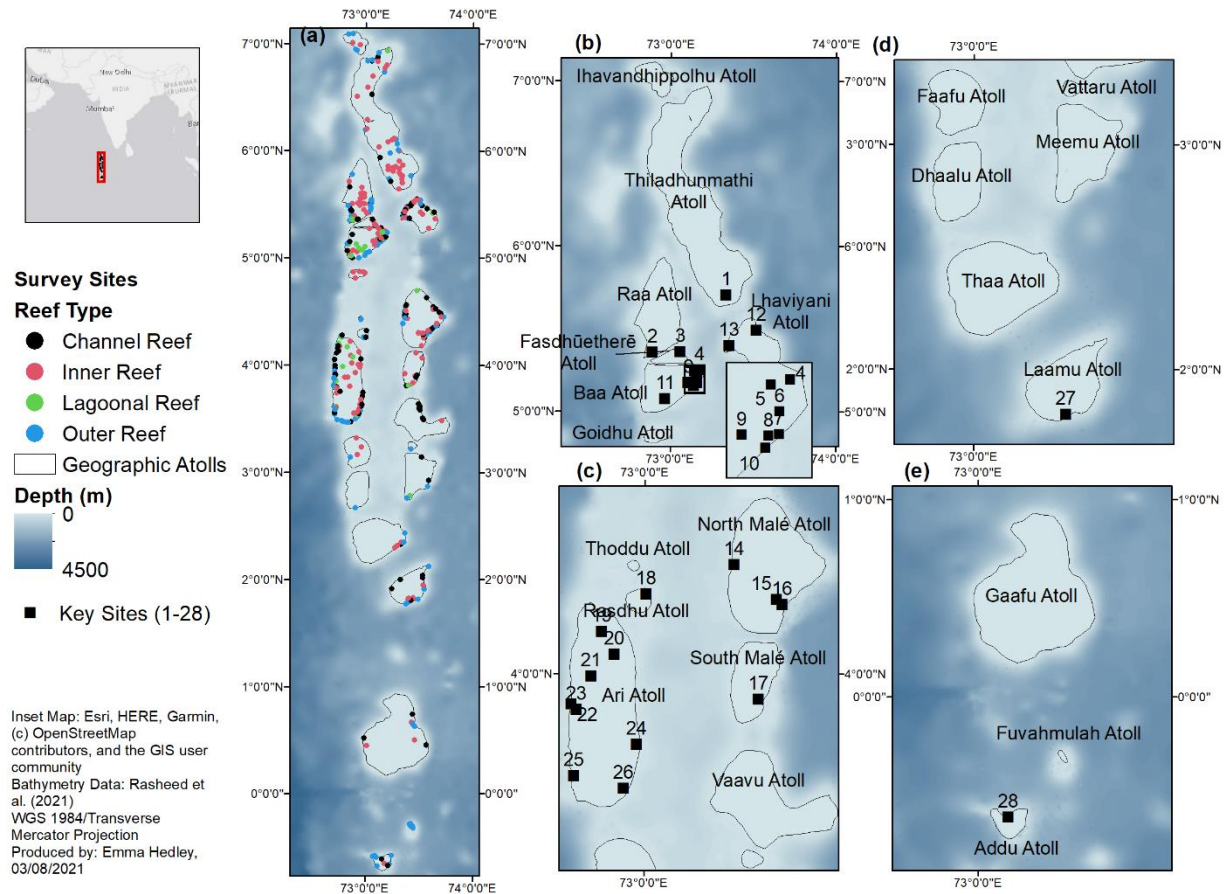


Figure 1. Maldivian geographic atolls with (a) all survey sites coloured by reef type, (b) key sites in the north and north-central regions, (c) key sites in the central region, (d) key sites in the south-central region, and (e) key sites in the southern region. Key site numbers refer to sites listed in Tables 1-3.

Photographs of the manta rays' unique ventral spot patterns, which can be used to identify the individual animal throughout its life (Figure 2), were collected using freediving or SCUBA diving, and trained MMCP researchers identified individuals by visual comparison to the MMCP's photo database (Kitchen-Wheeler, 2010; Marshall and Pierce, 2012). This study defines a sighting as a confirmed photo-identification (photo ID) of an individual manta ray in a certain location on a given day. During an encounter, when possible, the manta ray's photo ID and primary behaviour were recorded, with behaviour classified by observers as feeding, cleaning, cruising, or courtship. Maturity status was assigned to individuals sighted using physiological indicators evidenced in the identification photos and size estimates, with different indicators used for males and females. Male maturity was visually indicated by the size of the claspers, with males considered mature when their claspers were enlarged and calcified, and extended well beyond the individual's pelvic fins, or at disc widths >270 cm; female maturity was visually

indicated by the presence of mating scars or observed pregnancies, or at disc widths >320 cm (Figure 2) (Stevens, 2016). Males were classed as juveniles when their claspers had not yet begun to calcify and enlarge, and females were classed as juveniles when they had no visible mating scars or pregnancies and were <320 cm in disc width (Stevens, 2016). Individuals in their first year of life were considered young of year (YoY) and were classed based on estimated size, with YoY having a disc width <220 cm (G. Stevens, pers. comm., 2021).

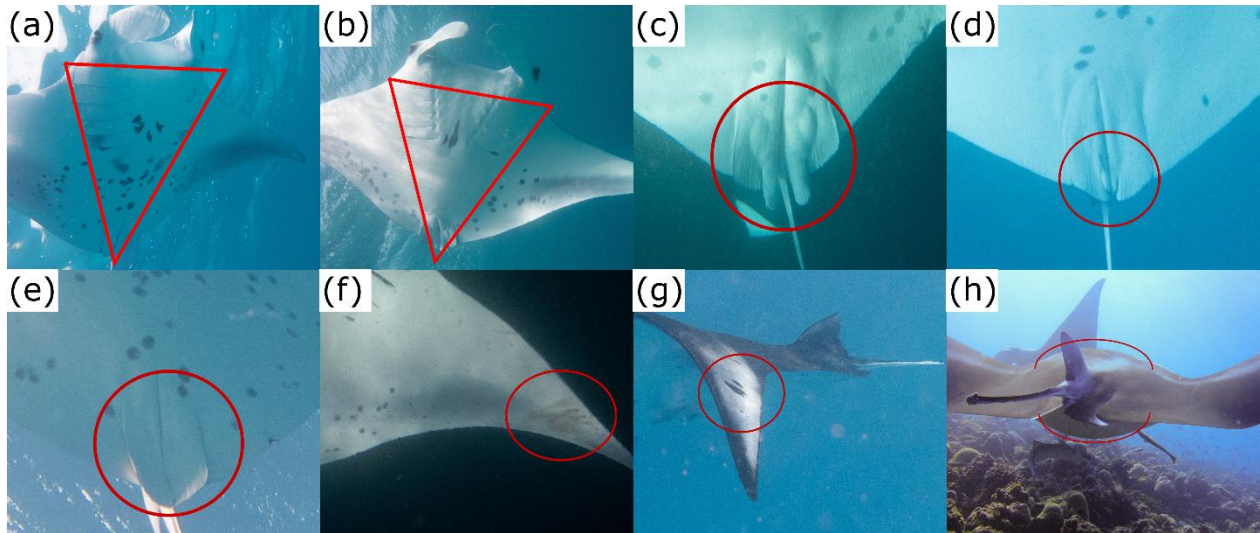


Figure 2. Morphological characteristics of reef manta rays that can be used to determine individual identification and maturity status. The (a-b) unique ventral spot pattern is used to identify individuals. Males have visible claspers that (c) are enlarged and calcified at maturity (adult) and (d) have not yet enlarged or calcified (juvenile). Females (e) do not have claspers but the presence of (f) ventral mating scars, (g) dorsal mating scars, or (h) visible pregnancy indicate maturity (adult).

2.3 Data Collation

The number of sightings of adults and juveniles for each behavioural activity (feeding and cleaning), and the number of sightings of YoY individuals displaying feeding behaviour, per site per day sightings occurred were compiled, along with the following associated environmental variables, all of which are thought to effect manta ray occurrence: (1) depth, (2) slope, (3) surface chlorophyll-a concentration, (4) sea surface temperature, (5) reef type, (6) side of atoll, and (7) season.

Gridded bathymetry data at a resolution of 0.35 arc-seconds (approximately 30 meters) were obtained from Rasheed *et al.*, 2021. Bathymetric data were used to calculate slope, or gradient, in degrees from 0–90 at the same 30 meter resolution by assessing the rate of change of depth values from each cell using the Spatial Analyst toolbox in ArcMap 10.7 (ESRI, 2018)

(Appendix I, Figure S1). Mean monthly 4 km resolution surface chlorophyll-a data were taken from the Copernicus-GlobColour programme provided by ACRI-ST (Garneison *et al.*, 2021) and monthly 0.01 degree latitude/longitude (approximately 1.1 km) sea surface temperature data were obtained from NASA's Group for High Resolution Sea Surface Temperature Multiscale Ultrahigh Resolution Level 4 analysis (NASA/JPL, 2015) (Appendix I, Figures S2 – S5).

The reef type of each location (channel reef, inner reef, outer reef, and lagoonal reef) was assigned based on observations recorded in the field by the MMCP. Due to the known seasonal migrations of reef manta rays from the eastern to western atoll edges (Anderson *et al.*, 2011; Harris *et al.*, 2020), each site was classed as east or west based on its location in the atoll following the methodology of Harris *et al.* (2020). Each sighting day was classified by season, with the NE monsoon season assumed to run from December through March (Julian days 1-90 and 335-366) and the SW monsoon assumed between May and October (Julian days 121-304) (Anderson *et al.*, 2011). Sightings that occurred in the months of April and November were classed as transitional season sightings.

2.4 Key Sites

Key reef manta ray sites were determined for each demographic group (adult, juvenile, and YoY) based on the total number of sightings recorded at known and surveyed sites across all years of data collection (1987-2019) (Stevens, 2016; Harris *et al.*, 2020). Sightings were split by demographic and key sites were determined to be those with at least 1% of all sightings of individuals within the analysed demographic group. Due to inconsistent records of site visits with no manta rays seen, key site determination was not standardised by effort.

2.5 Statistical Analysis

To evaluate if differences occurred between the daily number of sightings of juvenile and adult reef manta rays displaying all observed behaviours at different sites across all years of data collection (1987-2019), a 2 x 80 Pearson's Chi-squared test was performed in R version 4.0.2 (R Core Team, 2020). Due to low sample sizes at many sites, only sites with at least 50 sightings were used in the analysis. To allow for further evaluation of all sightings across all survey years at all sites, sites were then grouped by reef type and a 2 x 4 Pearson's Chi-squared test was performed.

Further investigation into environmental influences on daily sightings of each demographic group was performed separately for sightings of feeding and cleaning manta rays at all sites where sightings were recorded during MMCP survey years (2005-2019). Manta ray cleaning stations in the Maldives are generally smaller in extent than feeding sites, and surveys of cleaning manta rays are primarily conducted with an in-water search whilst most surveys of feeding manta rays are conducted by an on-vessel search across these larger areas. To account for this variation, a 100-meter buffer was built in ArcMap 10.7 (ESRI, 2018) for sites with observations of cleaning manta rays and a 500 meter buffer was built for sites with observations of feeding manta rays. Sea surface temperature and chlorophyll-a values, both with resolutions coarser than the site buffer sizes, were then extracted using the Sampling tool, and depth and slope were averaged across the buffer areas using the Zonal Statistics as Table tool in ArcMap 10.7. Environmental variables were plotted against one another to examine for collinearity (Appendix I, Figure S6).

A set of generalised additive models (GAMs) were used to identify important predictors of daily reef manta ray sightings for each demographic group (adults, juveniles, and YoY). All GAM models were created using the 'mgcv' package in R version 4.0.2 (Wood, 2011; R Core Team, 2020). The relationship between daily number of sightings for each demographic group and each behaviour was evaluated against separate smooth spline terms representing depth, slope, chlorophyll-a concentration, and sea surface temperature, a factor term representing reef type, and an interaction term representing seasonality between the side of the atoll and season. The interaction term was included due to the biological assumption that reef manta rays migrate between sites on the eastern and western atoll sides with the changing seasons (Anderson *et al.*, 2011; Harris *et al.*, 2020). A log link function was used and a negative binomial error distribution of sightings was assumed due to the large number of zero values in the data (Warton, 2005; Drexler and Ainsworth, 2013). Due to the small number of sightings of YoY individuals cleaning ($n=70$), no models were run for this group.

Further investigation was undertaken to understand the conditions that influence the probability that a sighting of a feeding manta ray is a juvenile. A GAM assuming a binomial distribution, where sightings of juveniles were classed as successes and sightings of adults were

classed as failures, was used. The model was fitted with separate smooth spline terms representing depth, slope, chlorophyll-a concentration, and sea surface temperature, a factor term representing reef type, and an interaction term between the side of the atoll and season representing known seasonal manta ray movements. A logit link function was used, and the counts of successes and failures were assumed to follow a binomial distribution (Appendix II).

Model assumptions were checked using diagnostic plots. Model selection was performed using Akaike information criterion (AIC) to determine the combination of environmental variables that best explained the observed patterns in the data. Models with different combinations of environmental co-variables were compared and the best fitting model was determined to be the one with the lowest AIC value.

Additional checks of whether models captured the variation in the data, as well as visual analysis of manta ray sightings distribution, were performed separately for each season. Mean seasonal values for chlorophyll-a and sea surface temperature were calculated across all MMCP survey years (2005-2019) for each site per season. These mean seasonal values were used along with the relevant environmental variables for each site to estimate manta ray sightings per season using the predict function of the 'mgcv' package in R version 4.0.2 (Wood, 2011; R Core Team, 2020). Estimated number of sightings for each site and each season, and the mean number of observed sightings for each season were compared to check whether fitted models captured the variation observed in the data. For the more populous north-central (Raa, Fasdhūetherē, Baa, Lhaviyani, and southern Thiladhunmathi Atolls) and central (Ari, Rashdu, North and South Malé, and Vaavu Atolls) regions, estimated sightings and mean observed sightings were plotted for each season in ArcMap version 10.7 (ESRI, 2018) to visualise distribution patterns.

3.0 Results

3.1 Manta Ray Sightings

A total of 47,568 sightings of 3,004 adult individuals, 22,906 sightings of 2,119 juvenile individuals, and 581 sightings of 256 YoY individuals were recorded on 3,947 days between 1987 and 2019 at 347 different sites. Thirty-eight percent ($n=18,096$) of adult sightings were cleaning and 58% ($n=27,367$) were feeding; the other 4% ($n=2,102$) displayed either cruising or courtship

behaviour, with an additional 3 sightings observed breaching or deceased. Twenty-four percent ($n=5,577$) of juvenile sightings were cleaning, 73% ($n=16,644$) were feeding, and the other 3% ($n=685$) were cruising or involved in courtship behaviour. Twelve percent ($n=70$) of YoY sightings were cleaning, 80% ($n=463$) were feeding, and 8% ($n=48$) were cruising.

Of these, a total of 72,829 sightings of 4,905 individuals were recorded on 3,899 days between 2005 and 2019, when the MMCP began its survey efforts. These included 17,970 sightings of adults cleaning, 5,568 sightings of juveniles cleaning, 27,353 sightings of adults feeding, 16,619 sightings of juveniles feeding, and 455 sightings of YoY feeding.

3.2 Key Sites

Seventy-nine percent ($n=37,740$) of all adult sightings occurred at 14 sites, 80% ($n=18,280$) of all juvenile sightings occurred at 20 sites, and 77% ($n=448$) of all YoY sightings occurred at 15 sites, with each of these sites having at least 1% percent of all recorded sightings of individuals of the corresponding demographic (Tables 1-3). Twenty-one of these sites were key sites for more than one demographic group and a total of 28 key sites were identified across all groups.

Table 1. Key sites for adult reef manta rays. The 14 key sites were determined as those with 1% or more of the total recorded sightings of adult individuals (1987-2019). Site numbers correspond to Figure 1.

Site Name	Site	Atoll	Sightings	% Total Sightings	Individuals	Reef Type	Side of Atoll
Reethi Falhu	4	Baa	1085	2.3	369	Lagoonal	E
Veyofushi Falhu	5	Baa	1022	2.1	294	Lagoonal	E
Hurai Faru	6	Baa	1015	2.1	318	Channel	E
Hanifaru Beyru	7	Baa	1101	2.3	410	Outer	E
Hanifaru Bay	8	Baa	18612	39.1	1112	Channel	E
Dhigu Thila	9	Baa	565	1.2	378	Inner	E
Dharavandhoo Corner	10	Baa	1414	3	399	Outer	E
Rasfari North	14	North Malé	1903	4	290	Outer	W
Sunlight Faru	15	North Malé	456	1	156	Inner	E
Lankan Beyru	16	North Malé	4657	9.8	419	Outer	E
Moofushi Bojmhadi	22	Ari	898	1.9	215	Outer	W
Dhiggaru Kandu	24	Ari	1001	2.1	204	Channel	E
Rangali Madivaru	25	Ari	1577	3.3	229	Outer	W
Hithadhoo Corner	27	Laamu	2434	5.1	73	Outer	E

Table 2. Key sites for juvenile reef manta rays. The 20 key sites were determined as those with 1% or more of the total recorded sightings of juvenile individuals (1987-2019). Site numbers correspond to Figure 1.

Site Name	Site	Atoll	Sightings	% Total Sightings	Individuals	Reef Type	Side of Atoll
Maamunagau Falhu	2	Raa	384	1.7	89	Lagoonal	W
Bathalaa Kandu	3	Fasdhüetherē	498	2.2	95	Channel	E
Reethi Falhu	4	Baa	1070	4.7	309	Lagoonal	E
Veyofushi Falhu	5	Baa	1296	5.7	256	Lagoonal	E
Hurai Faru	6	Baa	409	1.8	190	Channel	E
Hanifaru Beyru	7	Baa	299	1.3	137	Outer	E
Hanifaru Bay	8	Baa	8519	37.2	719	Channel	E
Dharavandhoo Corner	10	Baa	274	1.2	119	Outer	E
Fushifaru Kandu	12	Lhaviyani	261	1.1	82	Channel	E
Dhanifaru	13	Lhaviyani	348	1.5	116	Inner	W
Lankan Beyru	16	North Malé	498	2.2	118	Outer	E
Veligandu Kandu	18	Rasdhu	277	1.2	62	Channel	E
Maayafushi Falhu	20	Ari	252	1.1	30	Lagoonal	E
Fesdu Falhu	21	Ari	221	1	28	Lagoonal	W
Moofushi Bojamhadi	22	Ari	581	2.5	115	Outer	W
Maavaru Falhu	23	Ari	488	2.1	113	Lagoonal	W
Dhiggaru Kandu	24	Ari	578	2.5	99	Channel	E
Dhigurah Falhu	26	Ari	653	2.9	130	Lagoonal	E
Hithadhoo Corner	27	Laamu	1079	4.7	54	Outer	E
Mudakan	28	Addu	295	1.3	38	Channel	W

Table 3. Key sites for YoY reef manta rays. The 15 key sites were determined as those with 1% or more of the total recorded sightings of YoY individuals (1987-2019). Site numbers correspond to Figure 1.

Site Name	Site	Atoll	Sightings	% Total Sightings	Individuals	Reef Type	Side of Atoll
Randheli Falhu	1	Thiladhunmathi	8	1.4	7	Inner	E
Maamunagau Falhu	2	Raa	120	20.7	21	Lagoonal	W
Reethi Falhu	4	Baa	38	6.6	18	Lagoonal	E
Veyofushi Falhu	5	Baa	8	1.4	5	Lagoonal	E
Hanifaru Bay	8	Baa	21	3.6	16	Channel	E
Maaneigaa	11	Baa	36	6.2	16	Lagoonal	W
Fushifaru Kandu	12	Lhaviyani	20	3.4	10	Channel	E
Dhanifaru	13	Lhaviyani	11	1.9	8	Inner	W
Guraidhoo Falhu	17	South Malé	10	1.7	5	Inner	E
Genburugau Falhu	19	Ari	28	4.8	16	Lagoonal	W
Maayafushi Falhu	20	Ari	28	4.8	8	Lagoonal	E
Maavaru Falhu	23	Ari	45	7.8	18	Lagoonal	W
Dhigurah Falhu	26	Ari	41	7.1	17	Lagoonal	E
Hithadhoo Corner	27	Laamu	7	1.2	3	Outer	E
Mudakan	28	Addu	19	3.3	10	Channel	W

3.3 Environmental Influences on Reef Manta Ray Sightings

Of the sites with at least 50 recorded sightings ($n=80$), a significant difference was observed between the daily number of sightings of juveniles and adults engaged in all behaviours ($X^2=7444$, $df=79$, $N=68490$, $p=0$). When all sites ($n=350$) were grouped by reef type, a significant difference was observed between daily sightings of juveniles and adults displaying all behaviours ($X^2=4100$, $df=3$, $N=70419$, $p=0$); juveniles were more likely than expected to be sighted in lagoonal reefs and less likely than expected to be observed on outer reefs, and the opposite was observed for adults (Figure 3).

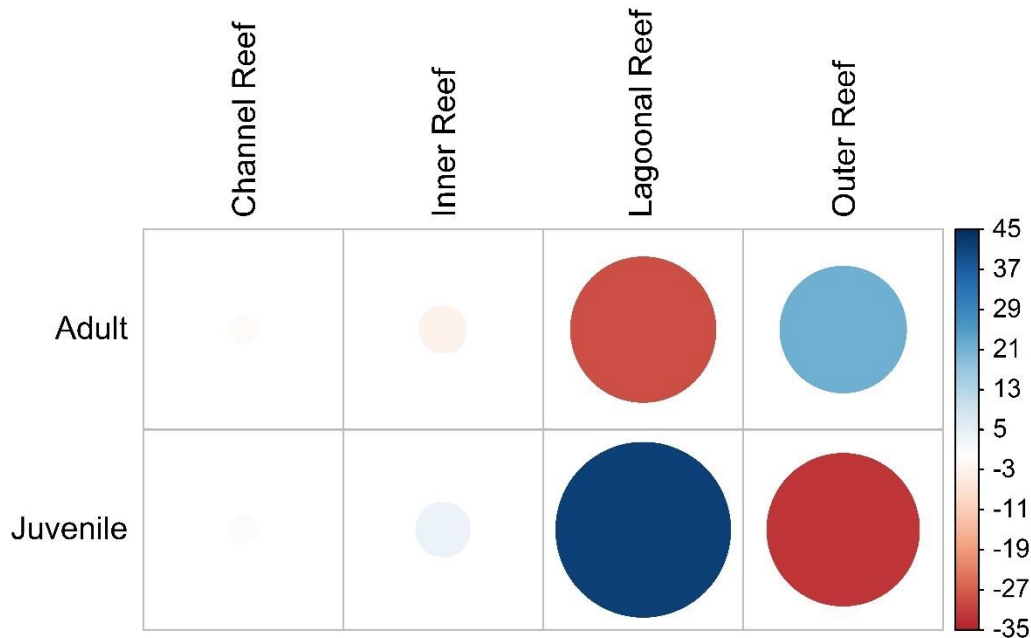


Figure 3. Chi-squared residual values representing the difference between the expected and observed sightings of juvenile and adult reef manta rays on days when manta rays were observed (1987-2019). Blue circles represent positive residuals and red circles represent negative residuals with darker shading and larger circles representing larger values.

When evaluating sightings of feeding adults on days and at sites where manta rays were sighted, the model selected by AIC criteria included explanatory variables: depth, slope, chlorophyll-a concentration, and sea surface temperature (Appendix II, Table S3). All explanatory co-variates were significant ($p < 0.05$) and the model explained 39.8% of deviance. More daily sightings were estimated to occur with the following conditions: slopes between five and ten degrees, shallower depths, chlorophyll-a concentrations greater than approximately 0.5 mg/m^3 , and sea surface temperatures below approximately 29.5°C . Slope had the largest effect size, and the most daily sightings were estimated for channel reefs and the lowest number of daily sightings were estimated for lagoonal reefs (Figure 4). In addition, more sightings were estimated during the SW monsoon season than during the NE monsoon season (Appendix I, Figure S8).

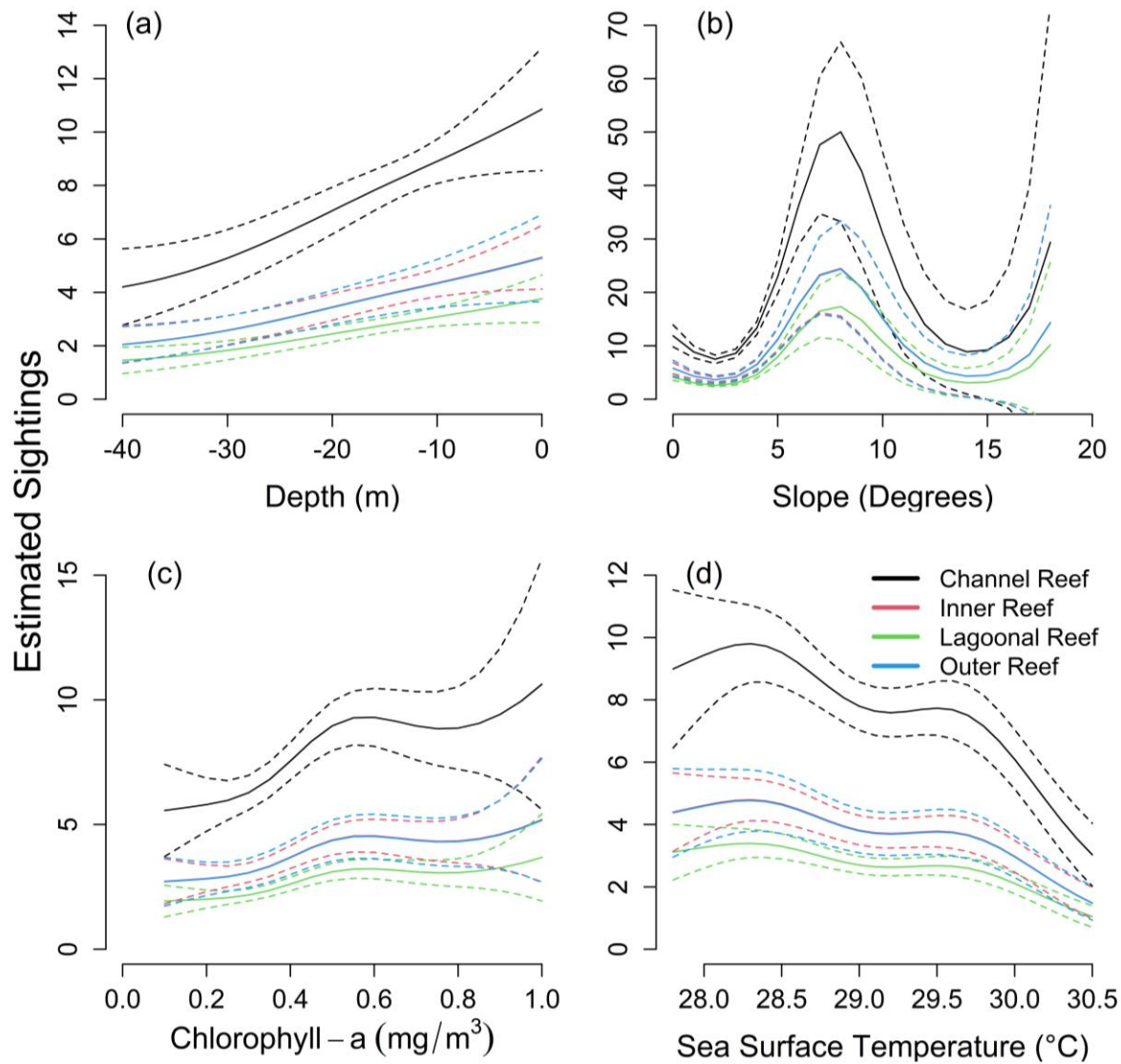


Figure 4. Estimated daily number of sightings of adult reef manta rays during the SW monsoon season displaying feeding behaviour with changing values of (a) depth, (b) slope, (c) chlorophyll-a concentration, and (d) sea surface temperature with each other co-variate held at its mean value. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of predicted sightings for channel reefs followed by inner reefs, outer reefs, and lagoonal reefs.

The model selected as the best-fit model by AIC when assessing daily sightings of feeding juveniles included depth, slope, chlorophyll-a concentration, and sea surface temperature as explanatory co-variates (Appendix II, Table S4). The model explained 23.3% of deviance and had significant smooth terms for depth and slope ($p < 0.05$). The largest number of daily sightings were estimated to occur at slopes between five and ten degrees and at shallower depths, with no clear trends in estimated sightings with changing chlorophyll-a concentrations or sea surface temperatures; more sightings were estimated for channel reefs, followed by lagoonal reefs,

inner reefs, and outer reefs (Figure 5). More daily sightings were predicted during the SW monsoon season (Appendix I, Figure S9).

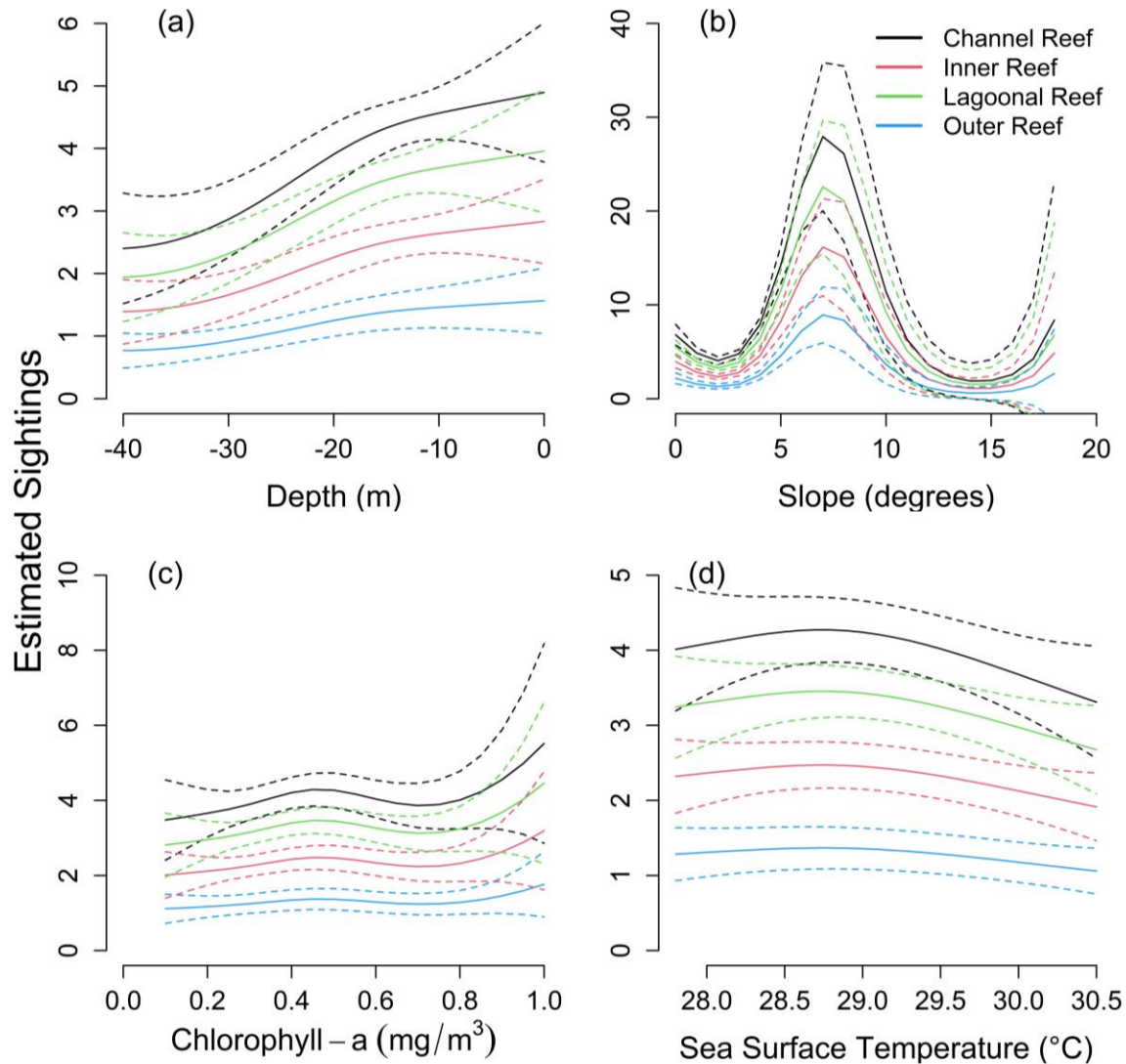


Figure 5. Estimated daily number of sightings of juvenile reef manta rays during the SW monsoon season displaying feeding behaviour with changing values of (a) depth, (b) slope, (c) chlorophyll-a concentration, and (d) sea surface temperature with each other co-variate held at its mean value. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of predicted sightings for channel reefs followed by lagoonal reefs, inner reefs, and outer reefs.

When assessing number of sightings of feeding YoY on days and at sites when sightings occurred, the model selected with AIC criteria included depth, chlorophyll-a concentration, and sea surface temperature as explanatory co-variates (Appendix II, Table S5). The model explained 20.1% of deviance and smooths of all three explanatory co-variates were significant ($p < 0.05$).

More sightings were estimated at depths between 10 and 20 meters, chlorophyll-a concentrations less than approximately 0.6 mg/m³, and at sea surface temperatures above 29°C (Figure 6). The largest number of sightings were estimated for lagoonal reefs followed by inner reefs, channel reefs, and outer reefs, and more sightings were estimated during the NE monsoon (Appendix I, Figure S10). The assumed east to west seasonal gradient was not evident for YoY, as the interaction term between season and side of atoll was not significant ($p>0.05$); however, differences between seasons were significant ($p<0.05$).

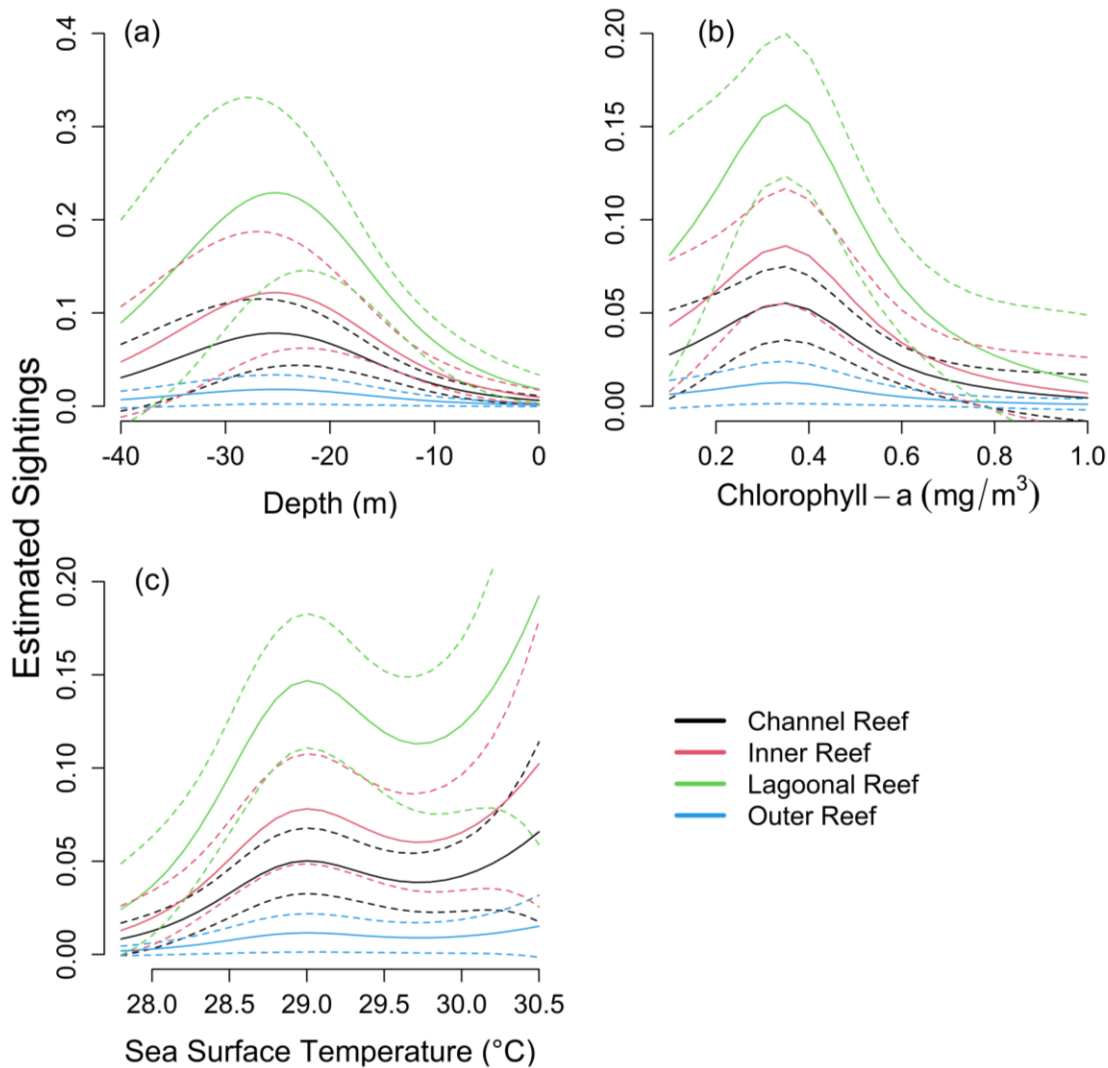


Figure 6. Estimated daily number of sightings of young of year (YoY) reef manta rays during the SW monsoon season displaying feeding behaviour with changing values of (a) depth, (b) chlorophyll-a concentration, and (c) sea surface temperature and each other co-variate held at its mean value. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of predicted sightings for lagoonal reefs followed by inner reefs, channel reefs, and outer reefs.

When assessing the probability that, if a manta ray is sighted, it is a juvenile, the model selected by AIC comparison included depth, slope, chlorophyll-a concentration, and sea surface temperature as explanatory variables (Appendix II, Table S6). The model explained 21.9% of deviance and had significant smooths for slope, chlorophyll-a, and sea surface temperature ($p < 0.05$). A weak positive correlation was estimated between the probability of a sighting being a juvenile and increasing sea surface temperature, and no clear trends were observed with changing depth, slope, or chlorophyll-a concentration. The estimated probability of a sighting being a juvenile was highest in lagoonal reefs, with it more likely that a sighting will be an adult in all other reef types ($\text{Pr}(\text{Juvenile}) < 0.5$) (Figure 7). The probability of a sighting being a juvenile was higher during the NE monsoon (Appendix I, Figure S11).

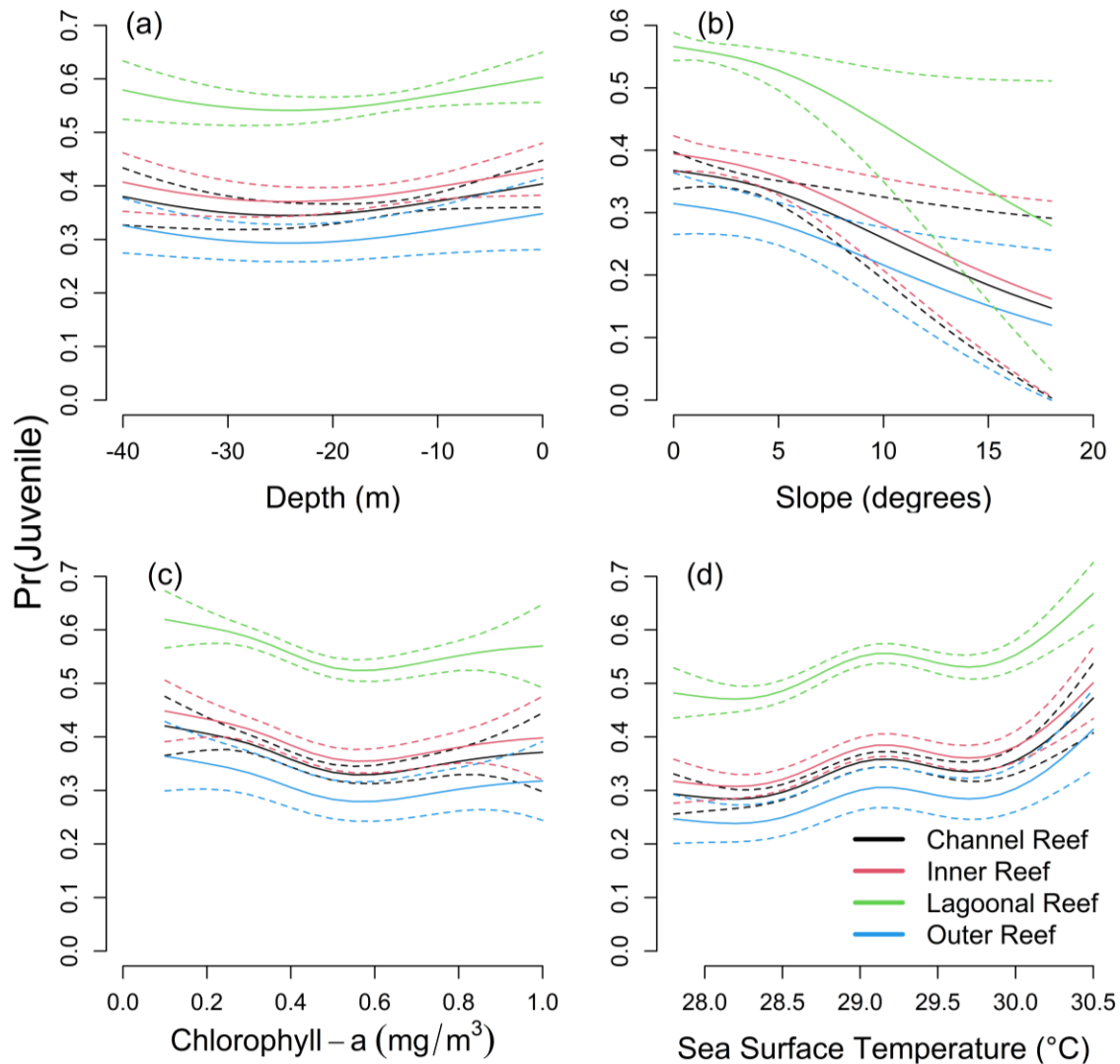


Figure 7. Estimated probability of a sighting of a feeding reef manta ray being a juvenile ($Pr(\text{Juvenile})$) during the SW monsoon with changing values of (a) depth, (b) slope, (c) chlorophyll-a and (d) sea surface temperature, and all other co-variables held at their mean values. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of predicted sightings for lagoonal reefs followed by inner reefs, channel reefs, and outer reefs.

Models evaluating sightings of adult or juvenile manta rays displaying cleaning behaviour did not provide a good fit to the observed data, explaining a low percentage of the deviance seen within the observations (<15% for adults and <5% for juveniles) (Appendix II, Tables S7 – S8). These models were not analysed further due to the poor model fit.

Of the juvenile-dominated key sites ($n=12$) (those with more estimated sightings of juveniles than adults in either season), 75% ($n=9$) were lagoonal reefs; however, of the key sites where estimated sightings of adults and juveniles were both high in either season ($n=6$), 83%

($n=5$) were channel reefs (Figure 8). The three key sites with the most estimated sightings of YoY were all lagoonal reefs.

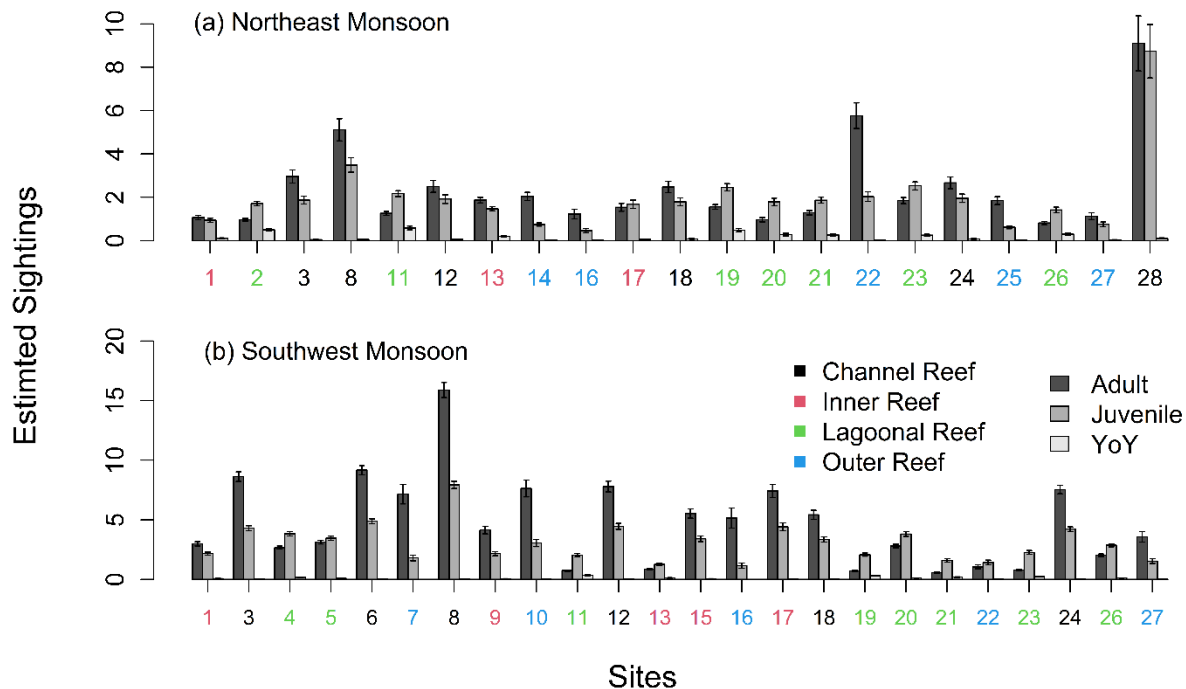


Figure 8. Estimated daily number of sightings at the key sites (Tables 1-3) for each demographic (Adult, Juvenile, and YoY) during (a) the NE monsoon and (b) the SW monsoon with model prediction error (1 SE).

3.4 Spatial Distribution of Reef Manta Ray Sightings

Overall, patterns of estimated sightings for adults displaying feeding behaviour matched with seasonal mean observations for both monsoon seasons (Appendix I, Tables S1 – S2). However, some clear discrepancies were observed in the north-central and central regions. Observed sightings during the SW monsoon at six sites in Raa Atoll were approximately two times higher than model estimates and were approximately five times higher at six sites in Baa Atoll (Figure 9). During the NE monsoon, observations were five times larger than estimated sightings at Hanifaru Bay (site 8) in Baa Atoll. Sites with the biggest discrepancy between mean seasonal observed sightings and seasonal predicted sightings, including Hanifaru Bay, were locations where mass aggregations have been observed, with up to 244 daily sightings recorded. On the other hand, the predicted number of sightings at nine sites in North Malé Atoll during the SW monsoon were 13 times larger than mean observed sightings.

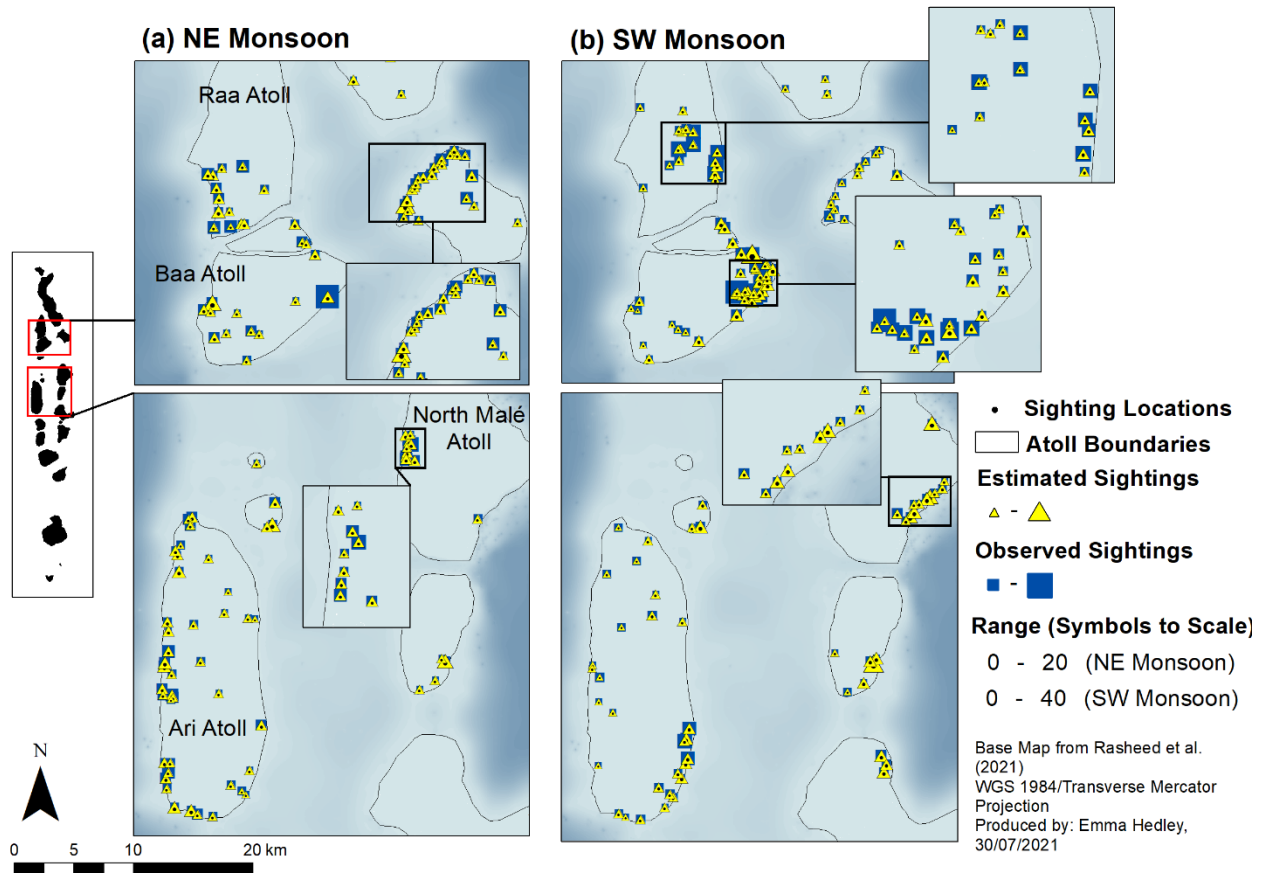


Figure 9. Number of adult reef manta ray sightings estimated by models (yellow triangles) at sites where manta rays have been observed and mean observed number of sightings (blue squares) (2005-2019) during (a) the NE monsoon season (December-March) and (b) the SW monsoon season (May-October). Map shows sightings of feeding behaviour in the north-central (top row) and central (bottom row) regions, where the majority of known reef manta ray sites are located. Symbols are on the same scale for each season, with squares and triangles of the same size when observed and estimated values are equal.

Similar patterns were observed for juveniles displaying feeding behaviour on days manta rays were observed (Figure 10). During the SW monsoon, mean seasonal observations at seven sites in Raa Atoll were approximately three times larger than model estimates and, at six sites in Baa Atoll, observed values were approximately three times larger than estimated values. During the NE monsoon, large discrepancies between observed and estimated sightings values occurred at Maamunagau Falhu (site 2) in Raa Atoll (five times as many sightings observed than models estimated) and at Hanifaru Bay (site 8) in Baa Atoll (twice as many sightings observed as estimated). As with the adults, these sites have been locations of large manta ray aggregations with, for example, up to 45 daily sightings recorded at Maamunagau Falhu and up to 244 daily

sightings recorded at Hanifaru Bay. Conversely, estimated sightings in North Malé Atoll were about six times higher at nine sites.

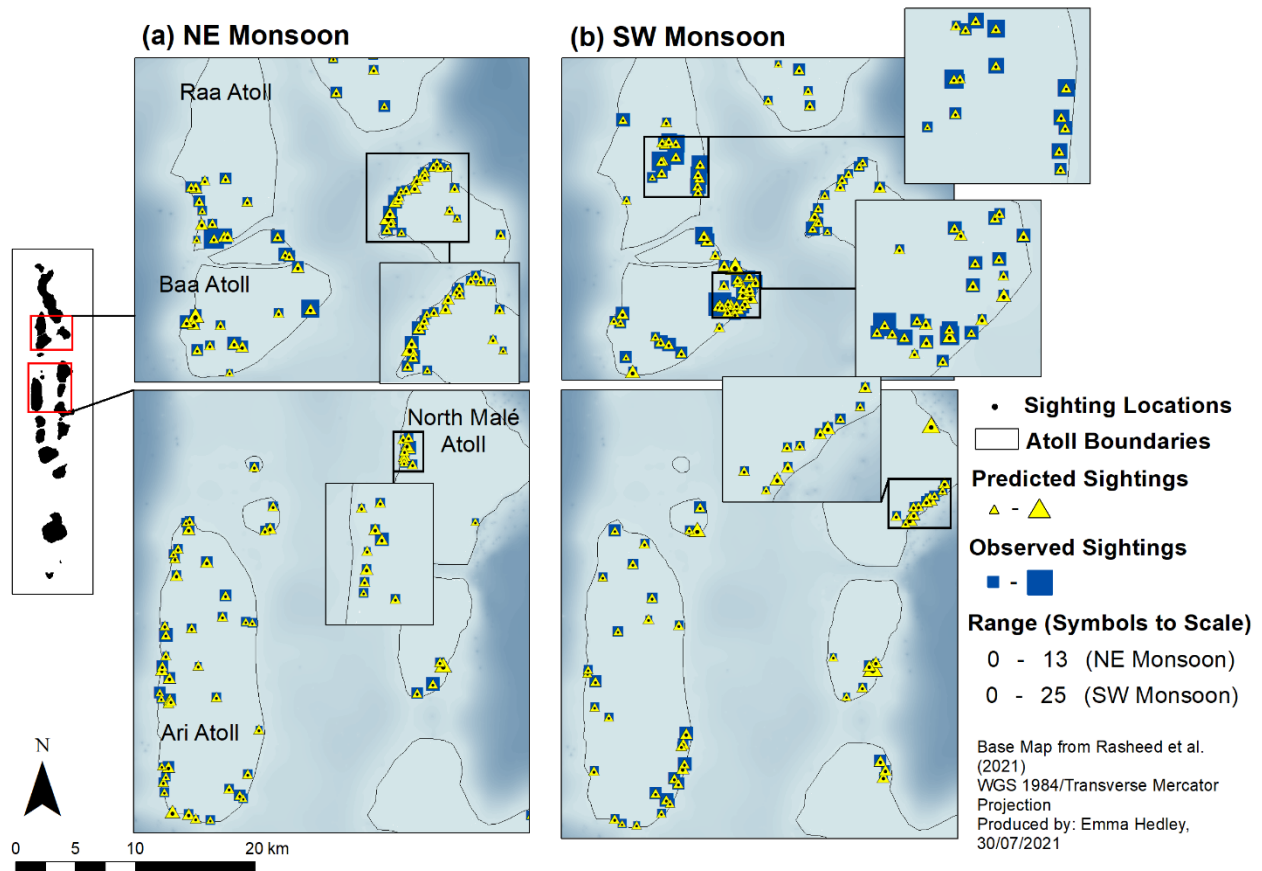


Figure 10. Number of juvenile reef manta ray sightings estimated by models (yellow triangles) at sites where manta rays have been observed and mean observed number of sightings (blue squares) (2005-2019) during (a) the NE monsoon season (December-March) and (b) the SW monsoon season (May-October). Map shows sightings of feeding behaviour in the north-central (top row) and central (bottom row) regions, where the majority of known reef manta ray sites are located. Symbols are on the same scale for each season, with squares and triangles of the same size when observed and estimated values are equal.

Overall, the number of sightings estimated by models for each season and the seasonal mean number of observed sightings of YoY individuals displaying feeding behaviour were lower than those for adults and juveniles. Discrepancies between model estimates and mean observed seasonal sightings existed across sites and varied substantially across regions (Figure 11). On average, observed sightings were 1.1 times larger than estimated sightings during the NE monsoon and two times larger during the SW monsoon.

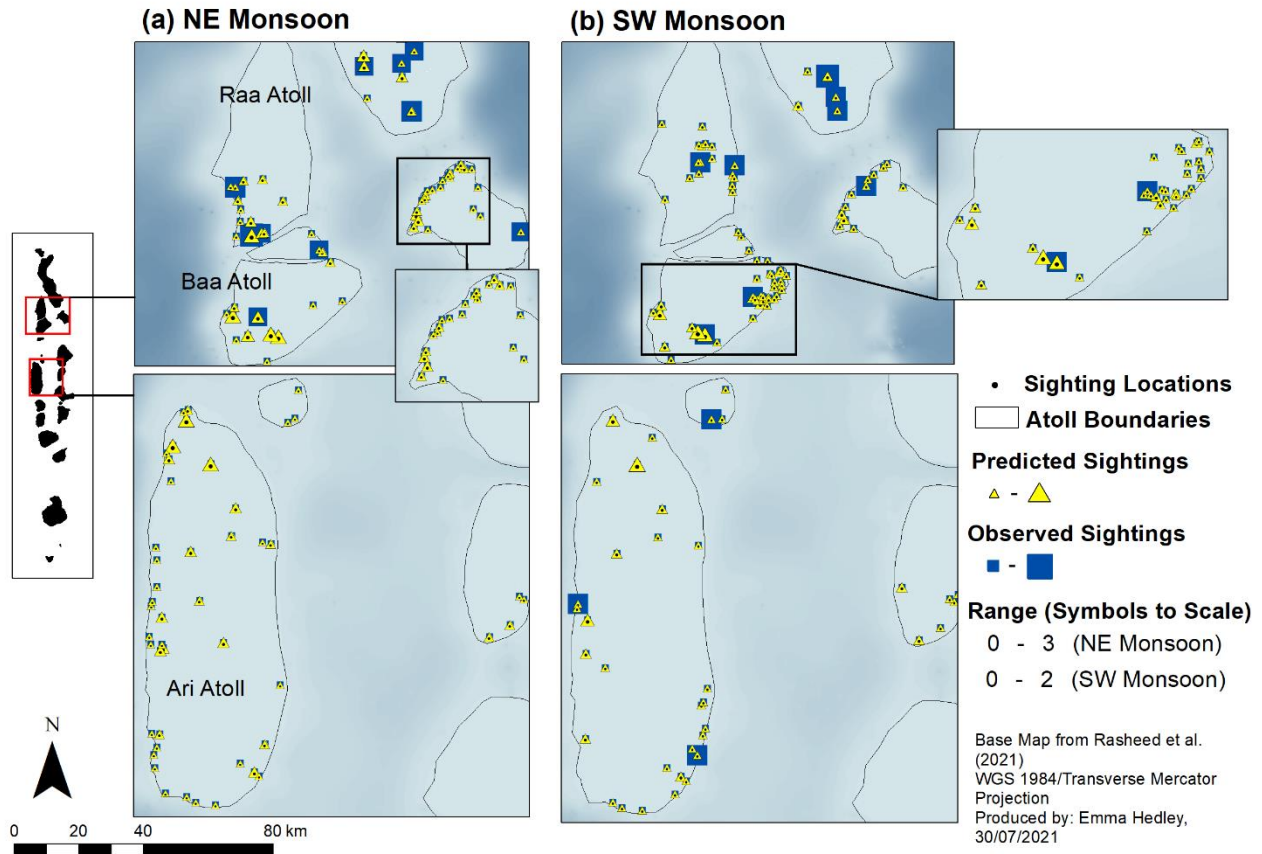


Figure 11. Number of YoY reef manta ray sightings estimated by models (yellow triangles) at sites where manta rays have been observed and mean observed number of sightings (blue squares) (2005-2019) during (a) the NE monsoon season (December-March) and (b) the SW monsoon season (May-October). Map shows sightings of feeding behaviour in the north-central (top row) and central (bottom row) regions, where the majority of known reef manta ray sites are located. Symbols are on the same scale for each season, with squares and triangles of the same size when observed and estimated values are equal.

4.0 Discussion

To elucidate ontogenetic variation in reef manta ray site use and distribution in the Maldives, generalised additive models were used to assess the influence of depth, slope, chlorophyll-a concentration, sea surface temperature, and reef type on the daily number of sightings of adult, juvenile, and YoY manta rays at sites where reef manta rays have been seen across the archipelago. This research helps to build upon previous findings that have shown age-based site use segregation in the Maldives at feeding sights by assessing a wider range of potential environmental influences, and it fills knowledge gaps surrounding the site use of juveniles and YoY individuals (Stevens, 2016; Stewart, Jaine, *et al.*, 2018). It also can be used to

help guide spatial management efforts by informing MPA designation at important manta ray sites.

Chi-squared test results confirmed site segregation between adults and juveniles displaying all behaviours and, when sites were grouped by reef type, juveniles were more likely than expected to be observed in lagoons whilst adults were more likely than expected to be observed on outer reefs. Models relating daily sightings of feeding manta rays with environmental conditions suggested that the number of sightings of adults and juveniles did not differ substantially with changing values of depth or slope, however, the number of sightings of adults was more affected by changing chlorophyll-a levels and sea surface temperatures when compared to juveniles. In addition, reef type use also varied between demographic groups. Models of feeding manta rays estimated substantially more sightings of adults in channel reefs than the other reef types, which is consistent with previous findings that, within feeding sites, adults were more likely than expected to be observed in channels (Stevens, 2016). When the juvenile demographic group was analysed independently, most sightings were estimated in channel reefs, however, when sightings of adults and juveniles were modelled together, estimates suggested that, in a lagoon, a sighting of a manta ray was more likely to be a juvenile. When estimating the probability of a manta ray sighting being a juvenile, reef type had the largest effect size and the majority of juvenile-dominated key sites were lagoonal reefs, further supporting the assumed importance of lagoonal reefs to the juvenile life stage.

Manta ray habitat use is likely driven by a trade-off between zooplankton, or food, availability and protection from predation, a trade-off common to marine species (Munsch *et al.*, 2016; Hussey *et al.*, 2017). The environmental predictors used in this study were selected due to their assumed ecological role with chlorophyll-a and sea surface temperature assumed to affect phytoplankton and, thus, zooplankton availability (Jamil *et al.*, 2014). Food availability is known to drive reef manta ray movements, with manta rays feeding at locations and times when zooplankton biomass is high and in some locations, animals have been observed travelling long distances offshore to take advantage of highly productive areas (Jaine *et al.*, 2014; Armstrong *et al.*, 2016). The atoll structure of the Maldives strongly influences food availability, with strong tidal currents carrying zooplankton into the atolls via channels, a process known to

occur in similar atoll environments in Australia and the Chagos Archipelago (Anderson *et al.*, 2011; Stevens, 2016; Green *et al.*, 2018; Sheehan *et al.*, 2019). Therefore, the significance of chlorophyll-a and sea surface temperature and the relative importance of channel reefs for feeding adult manta rays suggest that sightings and, thus, site use within this demographic group are driven by food availability.

Large predatory sharks, particularly bull (*Carcharhinus leucas*) and tiger (*Galeocerdo cuvier*) sharks, as well as false killer whales (*Pseudorca crassidens*), orcas (*Orcinus orca*), and 11 additional species of shark are known manta ray predators (Marshall and Bennett, 2010; Stevens *et al.*, 2020). These species primarily inhabit offshore waters and reef manta rays are more likely to be exposed to attacks in open water, which is indicated by lower reported rates of predation-related injuries in locations like the Maldives and Hawaii, where reef manta rays spend more time inshore, than in Mozambique, where manta rays forage further offshore (Marshall and Bennett, 2010; Deakos *et al.*, 2011; Stevens, 2016). Juvenile manta rays are more vulnerable to predation due to their smaller body sizes, so the more time they spend in protected, shallow areas, the lower the predation risk. This is evidenced by the quicker accumulation of injuries by juvenile reef manta rays in the Maldives and the fact that juveniles were 20% more likely to be observed with injuries than adults (Strike, 2020; Strike *et al.*, 2021, in progress). In addition, juvenile manta rays tagged in the Seychelles travelled smaller daily distances in comparison to adults, which is thought to be due, in part, to predator avoidance (Peel *et al.*, 2019).

The higher likelihood than expected of observing juvenile manta rays in lagoonal reefs, as well as the higher probability that a reef manta ray sighting will be a juvenile in a lagoon, reflect the greater need for predator avoidance within the juvenile demographic group. However, high food availability in channel reefs might, at times, outweigh the risk of predation for juveniles, as evidenced by the high estimated number of sightings of juveniles, the less site segregation suggested by chi squared results, and the occurrence of key sites of shared importance to adults and juveniles in channel reefs. It is likely that the sites where demographic segregation is not observed are locations of particularly high food availability and that juveniles might primarily occupy protected lagoonal habitats but foray into productive channel reefs when conditions are

good. Research in the nearby Chagos Archipelago indicate that juveniles face the same trade-off and prioritise predator avoidance, with juvenile reef manta rays observed having less pronounced diel vertical movements than adults and remaining long in shallow waters (Harris *et al.*, 2021).

When assessing the subset of the juvenile demographic with the smallest body sizes, the YoY, lagoonal reef type appeared to be a strong driver of sightings distribution. YoY are particularly small, with an average disc width at birth of 160 cm, making them especially vulnerable to predation (Stevens, 2016). Reef manta rays are estimated to grow quickly within the first year of their lives, however, before they reach larger sizes it is vital for these small animals to prioritise protection from predators (Stevens, 2016; G. Stevens, pers comm., 2021). Therefore, the strong influence of lagoons and the lower estimated sightings at high concentrations of chlorophyll-a indicate that these small individuals are prioritising predator avoidance instead of occupying more exposed areas with greater food availability. In addition, the signal of the expected seasonal east-west migration was not significant for these small manta rays, likely due to a combination of predator avoidance, lower swimming efficiency, and differing energetic requirements of these smaller individuals, as was suggested in the Seychelles reef manta ray population (Peel *et al.*, 2019).

The importance of lagoons to juvenile and, especially YoY, reef manta rays in the Maldives is similar to observations in Palmyra Atoll, where reef manta rays showed high reliance on lagoonal habitats and where manta rays measured inside the lagoon were significantly smaller than those measured in nearby channels (McCauley *et al.*, 2014). In addition to providing protection from predation, lagoonal environments are also able to trap plankton brought into the atoll by tidal currents, likely providing sufficient foraging opportunities for manta rays within the lagoons (McCauley *et al.*, 2014; Stevens, 2016; Sheehan *et al.*, 2019). However, lagoons are sensitive to habitat degradation, pollution, sedimentation, and are often areas of heavy human activity, such as fishing and boat movement (McCauley *et al.*, 2014; Stewart, Jaine, *et al.*, 2018). Furthermore, the Maldivian pole and line tuna fishery depends on the fishing of small fish, primarily silver sprat (*Spratelloides gracilis*) from atoll lagoons, to be used as live bait, with the traditional baitfish fishery largely unregulated (Jauharee *et al.*, 2015; Miller *et al.*, 2017). For the

tuna fishery to retain its Marine Stewardship Council (MSC) eco certification, it must ensure low interaction between the livebait fishery and endangered, threatened, and protected species (Jauharee *et al.*, 2015; Stevens and Froman, 2018). Protection of lagoonal habitats from these threats is, therefore, of high importance for reef manta ray conservation and local fisheries.

Many species of elasmobranch, including manta rays, are known to utilise nursery habitats during the particularly vulnerable first year of their lives: for sharks and rays, nursery areas are sites where YoY are more commonly encountered and show higher site fidelity than the mean across all other areas, and are areas that are used repeatedly across years (Heupel *et al.*, 2007). Seven nursery areas have been described for manta rays globally (Indonesia, Gulf of Mexico, and Florida, USA): two of these nursery areas support oceanic or Caribbean manta rays and five are used by reef manta rays (Stewart, Nuttall, *et al.*, 2018; Germanov *et al.*, 2019; Pate and Marshall, 2020; Setyawan *et al.*, 2020). Of the five reef manta ray nurseries formally described, four are located in Raja Ampat, Indonesia, including three shallow lagoons and one nearshore coastal reef, and the other is in Nusa Penida, Indonesia, and is a shallow, semi-enclosed bay (Germanov *et al.*, 2019; Setyawan *et al.*, 2020). The increases in estimated YoY sightings with increased sea surface temperature observed in this study reflect findings in other elasmobranch species that juveniles in confined nursery habitats spend more time than adults above the species' optimal temperature (Lear *et al.*, 2019). Patterns observed in YoY in this study are consistent with those observed in other regions, suggesting that reef manta rays are likely using nursery areas in the Maldives.

Cleaning is another crucial behaviour of reef manta rays, however, models aiming to explore the environmental influences on sightings of cleaning manta rays in each demographic did not fit the data well enough to be used in analysis. The environmental co-variables selected for these models were the same as for models assessing feeding behaviour, as it has been shown in some locations that manta rays time their visits to cleaning stations when conditions are not optimal for feeding (O'Shea *et al.*, 2010; Jaine *et al.*, 2012; Peel *et al.*, 2019; Harris and Stevens, 2021). However, the poor model fit indicates that there are likely additional influences that operate at different scales on sightings of cleaning reef manta rays. First, manta ray visits to cleaning stations rely upon a combination of cleaning and feeding effectiveness; reef manta ray feeding

effectiveness is driven by plankton availability and concentration whilst cleaning effectiveness depends upon the ability of the cleaner wrasse to clean, and the cleaning-feeding decision has been shown to occur over an hourly time scale (Barr and Abelson, 2019). Analysis in the Philippines suggested that cleaning behaviour was more likely to be observed in low light conditions, due to scattered plankton reducing feeding efficiency, and at low water flow, as cleaner wrasse are unable to effectively clean when water flow is too fast (Barr and Abelson, 2019). Second, studies in eastern Australia highlighted the importance of tidal cycles, which operate on fine temporal scales, in driving manta ray cleaning patterns, with cleaning more likely to be observed on tides that are less favourable to feeding (O'Shea *et al.*, 2010; Jaine *et al.*, 2012). Third, manta rays also utilise cleaning station areas for social and reproductive purposes, and may switch between cleaning and these other activities during a cleaning station visit (Stevens *et al.*, 2018; Perryman *et al.*, 2019). Future research into the cleaning behaviour of manta rays in different demographic groups is suggested to be performed on a smaller temporal scale and with the inclusion, if possible, of light level, tide, and water flow as explanatory variables.

Model estimates were shown to be, for the most part, reliable, as the estimates overall matched mean observed sightings. However, it is important to note that there were several areas where clear discrepancies were noticed: in southeastern North Malé Atoll, model estimates were larger than observed means, and in southeastern Baa and southern Raa Atolls, observed means were larger than model estimates. These discrepancies might indicate that the use of the sighting day unit was not sufficient to correct for effort. The MMCP has high regular survey coverage during the SW monsoon in southeastern Baa Atoll and there are strong social networks between tour operators in the region, making it more likely that large numbers of observers are present and, therefore, can collect more sightings at locations where manta rays are seen. However, this does not explain the areas of noted discrepancies in Raa and North Malé Atolls, suggesting the influence of additional ecological factors.

Sites in Raa and Baa Atolls where models underestimated sightings were also locations where large aggregations of mass feeding manta rays have been observed. These periodic events, and the associated high number of sightings, may have inflated the mean observation

values in those locations. It is also possible that models were not able to fully account for the variation in sightings that occur during these intermittent events. In addition, tidal interactions with local reef topography are thought to be heavily influential on the few sites where mass feeding is observed, and this process operates on fine spatial and temporal scales (Harris and Stevens, 2021). Such local influences were not incorporated into this study as it was designed to investigate sightings across the entire Maldivian archipelago. Wind speed and direction have also been shown to influence reef manta sightings in the Maldives, however, these explanatory variables were not included in this study due to a lack of available gridded wind data across all survey sites at a relevant scale (Harris *et al.*, 2020; Harris and Stevens, 2021). Future research focussing on smaller scale processes at the highlighted key sites would further enhance understanding of reef manta ray feeding aggregation site use, particularly at sites where current models underestimated.

On the other hand, models overestimated reef manta ray sightings at several sites in North Malé Atoll. One reason for this discrepancy could be that, although these sites provide suitable conditions for feeding reef manta rays, they are not utilised. Reef manta rays in the Maldives, and globally, are known to show strong site fidelity in their habitat usage and, therefore, may be less likely to seek out new habitat even if it meets the required criteria (Couturier *et al.*, 2018; Germanov *et al.*, 2019; Harris *et al.*, 2020). An analogous process has been suggested for metapopulations of breeding colonies of birds and mammals that show site fidelity (Matthiopoulos and Thomas, 2005). Many of the same previously mentioned environmental influences that could not be accounted for during the modelling process of this study might also explain why these sites are less favoured by feeding manta rays.

Overall, estimated sightings of YoY individuals varied more from observed mean sightings when compared with the other two demographic groups, and overall mean observed YoY sightings were larger than model estimates. As previously discussed for the other demographic groups, this may be influenced by additional environmental variables operating across different scales. Despite some model discrepancies, insights gained into YoY distribution are important, as these small individuals likely rely upon nursery areas but no focussed study has yet been performed to define specific reef manta ray nurseries in the Maldives. The spatial analysis

performed in this study can be used to guide future efforts in identifying and defining Maldivian reef manta ray nurseries.

Mapping of model estimates for all demographics in the north-central and central regions can also assist in spatial planning, as the maps provide a more thorough understanding of where higher number of manta rays are estimated to be seen, particularly with the high tourism presence in these regions (Ministry of Tourism, 2019). Maldivian reef manta rays have the highest incidence of anthropogenic injuries in areas with more tourism and, therefore, more fishing and boat traffic (Strike, 2020; Strike *et al.*, 2021, in preparation). Effective management in these busy regions can reduce the threat of sub-lethal and lethal injuries. In addition, increasing management efforts in lagoons with high numbers of sightings will protect the juvenile and YoY individuals that utilise these sensitive habitats, and can also support the valuable MSC certified tuna fishery by reducing potential conflict in lagoonal areas that serve as key manta ray sites, particularly as the demand for baitfish continues to rise (Jauharee *et al.*, 2015).

Marine management efforts in the Maldives are particularly focussed on the expansion of the national MPA network. The implementation of new protected areas in sites where estimated sightings of manta rays are high for each ontogenetic stage will help to protect important habitat for reef manta rays at all life stages, particularly the crucial juvenile stage. For MPAs to be most effective in protecting both the charismatic and vulnerable manta rays and the larger ecosystem upon which they depend, there are a number of considerations beyond location for managers to consider. The success of an MPA is shown to increase with the inclusion of each of five key features: large size (>100 km²), old (>10 years), isolated, no take, and well enforced (Edgar *et al.*, 2014). Currently, the majority of the Maldivian MPAs do not meet these criteria, with the nation's largest MPA only 42 km² and with a management plan and enforcement in only one MPA (Stevens and Froman, 2018). Within the Maldives, the expansion of MPAs should aim to incorporate all these features, with the most practical being the implementation of no take and well enforced MPAs. This would serve to reduce the key anthropogenic threats to Maldivian reef manta rays from fishing line entanglement, boat strikes, and unsustainable tourism (Stevens and Froman, 2018).

Ecotourism, a type of tourism that involves responsible travel that helps to support conservation, can provide positive ecological and economic benefits, however, it can also cause unintentional environmental damage (Krüger, 2005; Gallagher and Hammerschlag, 2011; O'Malley *et al.*, 2013; Stronza *et al.*, 2019). Such has been the case for tourism focussed specifically around charismatic marine megafauna, such as turtles, whales, sharks, and manta rays (Quiros, 2007; Anderson *et al.*, 2010; Meletis and Harrison, 2010; Gallagher and Hammerschlag, 2011; Parsons, 2012; Cressey, 2014; Venables *et al.*, 2016; Murray *et al.*, 2020). Within the Maldives, tourism indirectly drives an increased risk of boat strike, due to increased boat traffic, and a higher likelihood of fishing line entanglement, from recreational fishing excursions and increased food fish capture for the tourist market (Stevens and Froman, 2018). Swim-with-manta ray tourist experiences can also directly impact manta rays, and studies in Western Australia and the Maldives have shown that poor in-water conduct by snorkellers elicits negative behavioural responses in manta rays; this raises concern about the potential cumulative effects of feeding cessation, altered behaviour, or abandonment of important habitat areas (Venables *et al.*, 2016; Murray *et al.*, 2020). To mitigate these effects, MPA planning should include the mandate and enforcement of an in-water code of conduct for manta ray interactions and boat speed limits throughout the MPA, along with the inclusion and enforcement of no take areas (Venables *et al.*, 2016; Murray *et al.*, 2020).

The new understanding gained of the spatial distribution and environmental influences on reef manta ray sightings at different ontogenetic stages can assist in the allocation of MPAs across the Maldives. Conservation of important reef manta ray habitat, particularly sites important to the manta rays' sensitive juvenile stage, will aid in efforts to protect this vulnerable but valuable population by supporting the juveniles' chances of reaching maturity and successfully reproducing, which is key to maintaining the population size and health. Proper management and enforcement of tourism, boat movements, and fishing within current and future Maldivian MPAs will serve to protect not only reef manta rays but also the wider ecosystem and economy.

5.0 References

- Anderson, R. C., Adam, M. S. and Goes, J. I. (2011) 'From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives', *Fisheries Oceanography*, 20(2), pp. 104–113. doi: 10.1111/j.1365-2419.2011.00571.x.
- Anderson, R. C., Adam, M. S., Kitchen-Wheeler, A.-M. and Stevens, G. (2010) 'EXTENT AND ECONOMIC VALUE OF MANTA RAY WATCHING IN MALDIVES', *Tourism in Marine Environments*, 7(1), pp. 15–27. doi: 10.3727/154427310X12826772784793.
- Armstrong, A. O., Armstrong, A. J., Jaine, F. R. A., Couturier, L. I. E., Fiora, K., Uribe-Palomino, J., Weeks, S. J., Townsend, K. A., Bennett, M. B. and Richardson, A. J. (2016) 'Prey Density Threshold and Tidal Influence on Reef Manta Ray Foraging at an Aggregation Site on the Great Barrier Reef', *PLOS ONE*, 11(5), p. e0153393. doi: 10.1371/JOURNAL.PONE.0153393.
- Barr, Y. and Abelson, A. (2019) 'Feeding - cleaning trade-off: Manta ray "Decision-Making" as a conservation tool', *Frontiers in Marine Science*, 6(88). doi: 10.3389/fmars.2019.00088.
- Couturier, L. I. E., Marshall, A. D., Jaine, F. R. A., Kashiwagi, T., Pierce, S. J., Townsend, K. A., Weeks, S. J., Bennett, M. B. and Richardson, A. J. (2012) 'Biology, ecology and conservation of the Mobulidae', *Journal of Fish Biology*, pp. 1075–1119. doi: 10.1111/j.1095-8649.2012.03264.x.
- Couturier, L. I. E., Newman, P., Jaine, F. R. A., Bennett, M. B., Venables, W. N., Cagua, E. F., Townsend, K. A., Weeks, S. J. and Richardson, A. J. (2018) 'Variation in occupancy and habitat use of *Mobula alfredi* at a major aggregation site', *Marine Ecology Progress Series*, 599, pp. 125–145. doi: 10.3354/meps12610.
- Cressey, D. (2014) 'Ecotourism rise hits whales', *Nature*. Nature Publishing Group, p. 358. doi: 10.1038/512358a.
- Croll, D. A., Dewar, H., Dulvy, N. K., Fernando, D., Francis, M. P., Galván-Magaña, F., Hall, M., Heinrichs, S., Marshall, A., Mccauley, D., Newton, K. M., Notarbartolo-Di-Sciara, G., O'Malley, M., O'Sullivan, J., Poortvliet, M., Roman, M., Stevens, G., Tershy, B. R. and White, W. T. (2016) 'Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26, pp. 562–575. doi: 10.1002/aqc.2591.
- Deakos, M. H., Baker, J. D. and Bejder, L. (2011) 'Characteristics of a manta ray *Manta alfredi* -population off Maui, Hawaii, and implications for management', *Marine Ecology Progress Series*, 429, pp. 245–260. doi: 10.3354/meps09085.
- DEFRA (no date) *Global Ocean Alliance: 30by30 initiative - GOV.UK*. Available at: <https://www.gov.uk/government/topical-events/global-ocean-alliance-30by30-initiative/about> (Accessed: 1 August 2021).
- Drexler, M. and Ainsworth, C. H. (2013) 'Generalized Additive Models Used to Predict Species Abundance in the Gulf of Mexico: An Ecosystem Modeling Tool', *PLoS ONE*, 8(5), p. e64458. doi: 10.1371/journal.pone.0064458.

Dulvy, N. K., Pardo, S. A., Simpfendorfer, C. A. and Carlson, J. K. (2014) 'Diagnosing the dangerous demography of manta rays using life history theory', *PeerJ*, 2, p. e400. doi: 10.7717/peerj.400.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T. F., Berkhout, J., Buxton, C. D., Campbell, S. J., Cooper, A. T., Davey, M., Edgar, S. C., Försterra, G., Galván, D. E., Irigoyen, A. J., Kushner, D. J., *et al.* (2014) 'Global conservation outcomes depend on marine protected areas with five key features', *Nature*, 506, pp. 216–220. doi: 10.1038/nature13022.

EPA (2019) *Protected Areas of Maldives*. Available at: <https://en.epa.gov.mv/publications>.

ESRI (2018) 'ArcGIS Desktop'. Redlands, CA: Environmental Systems Research Institute.

Frisk, M. G., Miller, T. J. and Dulvy, N. K. (2005) 'Life Histories and Vulnerability to Exploitation of Elasmobranchs: Inferences from Elasticity, Perturbation and Phylogenetic Analyses', *Journal of Northwest Atlantic Fishery Science*, 35, pp. 27–45. doi: 10.2960/J.v35.m514.

Gallagher, A. J. and Hammerschlag, N. (2011) 'Global shark currency: the distribution, frequency, and economic value of shark ecotourism', *Current Issues in Tourism*, 14(8), pp. 797–812. doi: 10.1080/13683500.2011.585227.

Garnesson, P., Mangin, A. and Bretagnon, M. (2021) 'Quality User Guide, Ocean Colour Production Centre, Satellite Observation GlobColour-Copernicus Products'. Available at: http://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=OCEANCOLOUR_GLO_CHL_L3_NRT_OBSERVATIONS_009_032.

Germanov, E. S., Bejder, L., Chabanne, D. B. H., Dharmadi, D., Hendrawan, I. G., Marshall, A. D., Pierce, S. J., van Keulen, M. and Loneragan, N. R. (2019) 'Contrasting Habitat Use and Population Dynamics of Reef Manta Rays Within the Nusa Penida Marine Protected Area, Indonesia', *Frontiers in Marine Science*, 6, p. 215. doi: 10.3389/fmars.2019.00215.

Green, R. H., Lowe, R. J. and Buckley, M. L. (2018) 'Hydrodynamics of a Tidally Forced Coral Reef Atoll', *Journal of Geophysical Research: Oceans*, 123, pp. 7084–7101. doi: 10.1029/2018JC013946.

Grubbs, R. D. (2010) 'Ontogenetic shifts in movements and habitat use', in Carrier, J. C., Musick, J. A., and Heithaus, M. R. (eds) *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*. Boca Raton: CRC Press, pp. 319–350. doi: 10.1201/9781420080483.

Harris, J. L., Hosegood, P., Robinson, E., Embling, C. B., Hilbourne, S. and Stevens, G. M. W. (2021) 'Fine-scale oceanographic drivers of reef manta ray (*Mobula alfredi*) visitation patterns at a feeding aggregation site', *Ecology and Evolution*, 11, pp. 4588–4604. doi: 10.1002/ece3.7357.

Harris, J. L., McGregor, P. K., Oates, Y. and 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', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30, pp. 1649–1664. doi: 10.1002/aqc.3350.

- Harris, J. L. and Stevens, G. M. W. (2021) 'Environmental drivers of reef manta ray (*Mobula alfredi*) visitation patterns to key aggregation habitats in the Maldives', *PLOS ONE*. Edited by J. Mourier, 16(6), p. e0252470. doi: 10.1371/journal.pone.0252470.
- Heppell, S. S., Caswell, H. and Crowder, L. B. (2000) 'Life Histories and Elasticity Patterns: Perturbation Analysis for Species with Minimal Demographic Data', *Ecology*, 81(3), pp. 654–665.
- Heupel, M. R., Carlson, J. K. and Simpfendorfer, C. A. (2007) 'Shark nursery areas: concepts, definition, characterization and assumptions', *Marine Ecology Progress Series*, 337, pp. 287–297. doi: 10.3354/meps337287.
- Hooker, S. K., Cañadas, A., Hyrenbach, K. D., Corrigan, C., Polovina, J. J. and Reeves, R. R. (2011) 'Making protected area networks effective for marine top predators', *Endangered Species Research*, 13, pp. 203–218. doi: 10.3354/esr00322.
- Hooker, S. K. and Gerber, L. R. (2004) 'Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna', *BioScience*, 54(1), pp. 27–39. doi: 10.1641/0006-3568(2004)054[0027:MRAATF]2.0.CO;2.
- Hussey, N. E., DiBattista, J. D., Moore, J. W., Ward, E. J., Fisk, A. T., Kessel, S., Guttridge, T. L., Feldheim, K. A., Franks, B. R., Gruber, S. H., Weideli, O. C. and Chapman, D. D. (2017) 'Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions', *Proceedings of the Royal Society B: Biological Sciences*, 284, p. 20170166. doi: 10.1098/RSPB.2017.0166.
- Jaine, F. R. A., Couturier, L. I. E., Weeks, S. J., Townsend, K. A., Bennett, M. B., Fiora, K. and Richardson, A. J. (2012) 'When Giants Turn Up: Sighting Trends, Environmental Influences and Habitat Use of the Manta Ray *Manta alfredi* at a Coral Reef', *PLoS ONE*, 7(10), p. e46170. doi: 10.1371/JOURNAL.PONE.0046170.
- Jaine, F. R. A., Rohner, C. A., Weeks, S. J., Couturier, L. I. E., Bennett, M. B., Townsend, K. A. and Richardson, A. J. (2014) 'Movements and habitat use of reef manta rays off eastern Australia: Offshore excursions, deep diving and eddy affinity revealed by satellite telemetry', *Marine Ecology Progress Series*, 510, pp. 73–86. doi: 10.3354/MEPS10910.
- Jamil, T., Kruk, C. and Braak, C. J. F. ter (2014) 'A Unimodal Species Response Model Relating Traits to Environment with Application to Phytoplankton Communities', *PLOS ONE*, 9(5), p. e97583. doi: 10.1371/JOURNAL.PONE.0097583.
- Jauharee, A. R., Neal, K. and Miller, K. I. (2015) *Maldives Pole-and-line Tuna Fishery: Livebait Fishery Review*. Available at: <https://www.mrc.gov.mv/assets/Uploads/December-2015-Maldives-Pole-and-line-Tuna-Fishery-Livebait-Fishery-Review-2015.pdf> (Accessed: 7 August 2021).
- Kitchen-Wheeler, A. M. (2010) 'Visual identification of individual manta ray (*Manta alfredi*) in the Maldives Islands, Western Indian Ocean', *Marine Biology Research*, 6(4), pp. 351–363. doi: 10.1080/17451000903233763.

- Kitchen-Wheeler, A. M., Ari, C. and Edwards, A. J. (2011) 'Population estimates of Alfred mantas (*Manta alfredi*) in central Maldives atolls: North Male, Ari and Baa', *Environmental Biology of Fishes*, 93, pp. 557–575. doi: 10.1007/s10641-011-9950-8.
- Krüger, O. (2005) 'The role of ecotourism in conservation: panacea or Pandora's box?', *Biodiversity and Conservation*, 14, pp. 579–600. doi: 10.1007/S10531-004-3917-4.
- Lear, K. O., Whitney, N. M., Morgan, D. L., Brewster, L. R., Whitty, J. M., Poulakis, G. R., Scharer, R. M., Guttridge, T. L. and Gleiss, A. C. (2019) 'Thermal performance responses in free-ranging elasmobranchs depend on habitat use and body size', *Oecologia*, 191, pp. 829–842. doi: 10.1007/S00442-019-04547-1.
- Marshall, A., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Herman, K., Jabado, R. W., Liu, K. M., Pacoureau, N., Rigby, C. L., Romanov, E. and Sherley, R. B. (2019) 'Mobula alfredi', *The IUCN Red List of Threatened Species*, e.T195459A. doi: <http://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T195459A68632178.en> Disclaimer.
- Marshall, A. D. and Bennett, M. B. (2010) 'The frequency and effect of shark-inflicted bite injuries to the reef manta ray *Manta alfredi*', *African Journal of Marine Science*, 32(3), pp. 573–580. doi: 10.2989/1814232X.2010.538152.
- Marshall, A. D. and Pierce, S. J. (2012) 'The use and abuse of photographic identification in sharks and rays', *Journal of Fish Biology*, 80, pp. 1361–1379. doi: 10.1111/j.1095-8649.2012.03244.x.
- Matthiopoulos, J. and Thomas, L. (2005) 'Metapopulation consequences of site fidelity for colonially breeding mammals and birds', *Journal of Animal Ecology*, 74, pp. 716–727. doi: 10.1111/J.1365-2656.2005.00970.X.
- McCauley, D. J., DeSalles, P. A., Young, H. S., Papastamatiou, Y. P., Caselle, J. E., Deakos, M. H., Gardner, J. P. A., Garton, D. W., Collen, J. D. and Micheli, F. (2014) 'Reliance of mobile species on sensitive habitats: A case study of manta rays (*Manta alfredi*) and lagoons', *Marine Biology*, 161, pp. 1987–1998. doi: 10.1007/s00227-014-2478-7.
- MEE (Ministry of Environment and Energy) (2015) *National Biodiversity Strategy and Action Plan 2016-2025*. Male. Available at: <https://www.environment.gov.mv/v2/en/download/4318>.
- MEE (Ministry of Environment and Energy) (2016) *STATE OF THE ENVIRONMENT 2016*. Male. Available at: <https://www.environment.gov.mv/v2/en/download/4270> (Accessed: 7 February 2021).
- Meletis, Z. A. and Harrison, E. C. (2010) 'Tourists and turtles: Searching for a balance in Tortuguero, Costa Rica', *Conservation and Society*, 8(1), pp. 26–43. doi: 10.4103/0972-4923.62678.
- Miller, K. I., Nadheeh, I., Riyaz Jauharee, A., Anderson, R. C. and Shiham Adam, M. (2017) 'Bycatch in the Maldivian pole-and-line tuna fishery', *PLoS ONE*, 12(5), p. e0177391. doi: 10.1371/journal.pone.0177391.

- Ministry of Tourism (2019) *Tourism Yearbook 2019*. Male. Available at: <https://www.tourism.gov.mv/dms/document/f5f522de183dde8f0f012884cecb1706.pdf>.
- Munsch, S. H., Cordell, J. R. and Toft, J. D. (2016) 'Fine-scale habitat use and behavior of a nearshore fish community: Nursery functions, predation avoidance, and spatiotemporal habitat partitioning', *Marine Ecology Progress Series*, 557, pp. 1–15. doi: 10.3354/MEPS11862.
- Murray, A., Garrud, E., Ender, I., Lee-Brooks, K., Atkins, R., Lynam, R., Arnold, K., Roberts, C., Hawkins, J. and Stevens, G. (2020) 'Protecting the million-dollar mantas; creating an evidence-based code of conduct for manta ray tourism interactions', *Journal of Ecotourism*, 19(2), pp. 132–147. doi: 10.1080/14724049.2019.1659802.
- NASA/JPL (2015) 'GHRST Level 4 MUR Global Foundation Sea Surface Temperature Analysis (v4.1)'. NASA Physical Oceanography DAAC. doi: 10.5067/GHGMR-4FJ04.
- NBS (National Bureau of Statistics) (2015) *Maldives Population and Housing Census 2014. Statistical Release 1: Population & Households*. Male. Available at: <http://statisticsmaldives.gov.mv/nbs/wp-content/uploads/2015/10/Census-Summary-Tables1.pdf> (Accessed: 4 August 2021).
- Notarbartolo-Di-Sciara, G. (1988) 'NATURAL HISTORY OF THE RAYS OF THE GENUS MOBULA IN THE GULF OF CALIFORNIA', *Fishery Bulletin*, 86(1), pp. 45–66.
- O'Malley, M. P., Lee-Brooks, K. and Medd, H. B. (2013) 'The Global Economic Impact of Manta Ray Watching Tourism', *PLoS ONE*, 8(5). doi: 10.1371/journal.pone.0065051.
- O'Malley, M. p., Townsend, K. A., Hilton, P., Heinrichs, S. and Stewart, J. D. (2017) 'Characterization of the trade in manta and devil ray gill plates in China and South-east Asia through trader surveys', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27, pp. 394–413. doi: 10.1002/aqc.2670.
- O'Shea, O. R., Kingsford, M. J. and Seymour, J. (2010) 'Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef', *Marine and Freshwater Research*, 61, pp. 65–73. doi: 10.1071/MF08301.
- Osgood, G., McCord, M. and Baum, J. (2020) 'Chondrichthyans as an umbrella species-complex for conserving South African biodiversity', *African Journal of Marine Science*, 42(1), pp. 81–93. doi: 10.2989/1814232X.2020.1729859.
- Parsons, E. C. M. (2012) 'The Negative Impacts of Whale-Watching', *Journal of Marine Biology*, pp. 1–9. doi: 10.1155/2012/807294.
- Pate, J. H. and Marshall, A. D. (2020) 'Urban manta rays: potential manta ray nursery habitat along a highly developed Florida coastline', *Endangered Species Research*, 43, pp. 51–64. doi: 10.3354/esr01054.

- Peel, L. R., Stevens, G. M. W., Daly, R., Daly, C. A. K., Lea, J. S. E., Clarke, C. R., Collin, S. P. and Meekan, M. G. (2019) 'Movement and residency patterns of reef manta rays *Mobula alfredi* in the Amirante Islands, Seychelles', *Marine Ecology Progress Series*, 621, pp. 169–184. doi: 10.3354/MEPS12995.
- Perryman, R. J. Y., Venables, S. K., Tapilatu, R. F., Marshall, A. D., Brown, C. and Franks, D. W. (2019) 'Social preferences and network structure in a population of reef manta rays', *Behavioral Ecology and Sociobiology*, 73, p. 114. doi: 10.1007/s00265-019-2720-x.
- Quiros, A. L. (2007) 'Tourist compliance to a Code of Conduct and the resulting effects on whale shark (*Rhincodon typus*) behavior in Donsol, Philippines', *Fisheries Research*, 84, pp. 102–108. doi: 10.1016/J.FISHRES.2006.11.017.
- R Core Team (2020) 'R: A language and environment for statistical computing'. Vienna, Austria: R Foundation for Statistical Computing. Available at: <https://www.r-project.org/>.
- Rasheed, S., Warder, S. C., Plancherel, Y. and Piggott, M. D. (2021) 'An Improved Gridded Bathymetric Data Set and Tidal Model for the Maldives Archipelago', *Earth and Space Science*, 8, p. e2020EA001207. doi: 10.1029/2020ea001207.
- Roberts, C. M., O'leary, B. C., Mccauley, D. J., Cury, P. M., Duarte, C. M., Lubchenco, J., Pauly, D., Sáenz-Arroyo, A., Sumaila, R., Wilson, R. W., Worm, B. and Castilla, J. C. (2017) 'Marine reserves can mitigate and promote adaptation to climate change', *Proceedings of the National Academy of Sciences of the United States of America*, 114(24), pp. 6167–6175. doi: 10.2307/26484187.
- Setyawan, E., Erdmann, M. V., Lewis, S. A., Mambrasar, R., Hasan, A. W., Templeton, S., Beale, C. S., Sianipar, A. B., Shidqi, R., Heuschkel, H., Ambafen, O., Izuan, M., Prasetya, M. F., Azizah, H., Hidayat, I. N., Pada, D. N., Muljadi, A., Pilkington- Vincett, R., Dharmadi, *et al.* (2020) 'Natural history of manta rays in the Bird's Head Seascape, Indonesia, with an analysis of the demography and spatial ecology of *Mobula alfredi* (Elasmobranchii: Mobulidae)', *Journal of the Ocean Science Foundation*, 36, pp. 49–83. doi: 10.5281/ZENODO.4396260.
- Sheehan, E. V., Hosegood, P., Game, C. A., Attrill, M. J., Tickler, D., Wootton, M., Johns, D. G. and Meeuwig, J. J. (2019) 'The Effect of Deep Oceanic Flushing on Water Properties and Ecosystem Functioning Within Atolls in the British Indian Ocean Territory', *Frontiers in Marine Science*, 6, p. 512. doi: 10.3389/FMARS.2019.00512.
- Stevens, G., Fernando, D., Dando, M. and Di Sciara, G. N. (2020) *Guide to the Manta and Devil Rays of the World, Guide to the Manta and Devil Rays of the World*. Princeton University Press. doi: 10.1515/9780691207216.
- Stevens, G. M. W. (2016) *Conservation and Population Ecology of Manta Rays in the Maldives*. University of York.
- Stevens, G. M. W. and Froman, N. (2018) 'The Maldives Archipelago', in Sheppard, C. (ed.) *World Seas: An Environmental Evaluation Volume II: The Indian Ocean to the Pacific*. Second Edi. Elsevier Ltd., pp. 211–236. doi: 10.1016/B978-0-08-100853-9.00010-5.

- Stevens, G. M. W., Hawkins, J. P. and Roberts, C. M. (2018) 'Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives', *Journal of Fish Biology*, 93, pp. 344–359. doi: 10.1111/jfb.13768.
- Stewart, J. D., Jaine, F. R. A., Armstrong, A. J., Armstrong, A. O., Bennett, M. B., Burgess, K. B., Couturier, L. I. E., Croll, D. A., Cronin, M. R., Deakos, M. H., Dudgeon, C. L., Fernando, D., Froman, N., Germanov, E. S., Hall, M. A., Hinojosa-Alvarez, S., Hosegood, J. E., Kashiwagi, T., Laglbauer, B. J. L., *et al.* (2018) 'Research Priorities to Support Effective Manta and Devil Ray Conservation', *Frontiers in Marine Science*, 5, p. 314. doi: 10.3389/fmars.2018.00314.
- Stewart, J. D., Nuttall, M., Hickerson, E. L. and Johnston, M. A. (2018) 'Important juvenile manta ray habitat at Flower Garden Banks National Marine Sanctuary in the northwestern Gulf of Mexico', *Marine Biology*, 165, p. 111. doi: 10.1007/s00227-018-3364-5.
- Strike, E. (2020) *Variations in sub-lethal injuries to manta rays in the Maldives*. University of York.
- Strike, E., Harris, J. L., Ballard, K., Hawkins, J., Stark, J. and Stevens, G. M. W. (2021) 'Sublethal injuries and physical abnormalities in manta rays *Mobula alfredi* and *M. birostris* in the Maldives'. In preparation.
- Stronza, A. L., Hunt, C. A. and Fitzgerald, L. A. (2019) 'Ecotourism for Conservation?', *Annual Review of Environment and Resources*, 44, pp. 229–253. doi: 10.1146/ANNUREV-ENVIRON-101718-033046.
- Venables, S., McGregor, F., Brain, L. and Van Keulen, M. (2016) 'Manta ray tourism management, precautionary strategies for a growing industry: a case study from the Ningaloo Marine Park, Western Australia', *Pacific Conservation Biology*, 22(4), pp. 295–300. doi: 10.1071/PC16003.
- Warton, D. I. (2005) 'Many zeros does not mean zero inflation: Comparing the goodness-of-fit of parametric models to multivariate abundance data', *Environmetrics*, 16, pp. 275–289. doi: 10.1002/env.702.
- Weng, K. C., Pedersen, M. W., Raye, G. A. Del, Caselle, J. E. and Gray, A. E. (2015) 'Umbrella species in marine systems: using the endangered humphead wrasse to conserve coral reefs', *Endangered Species Research*, 27, pp. 251–263. doi: 10.3354/ESR00663.
- Wood, S. N. (2011) 'Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models', *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(1), pp. 3–36. doi: 10.1111/J.1467-9868.2010.00749.X.
- Zacharias, M. A. and Roff, J. C. (2001) 'Use of focal species in marine conservation and management: a review and critique', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 11, pp. 59–76. doi: 10.1.1.535.1516.

Appendix I: Additional Figures and Tables

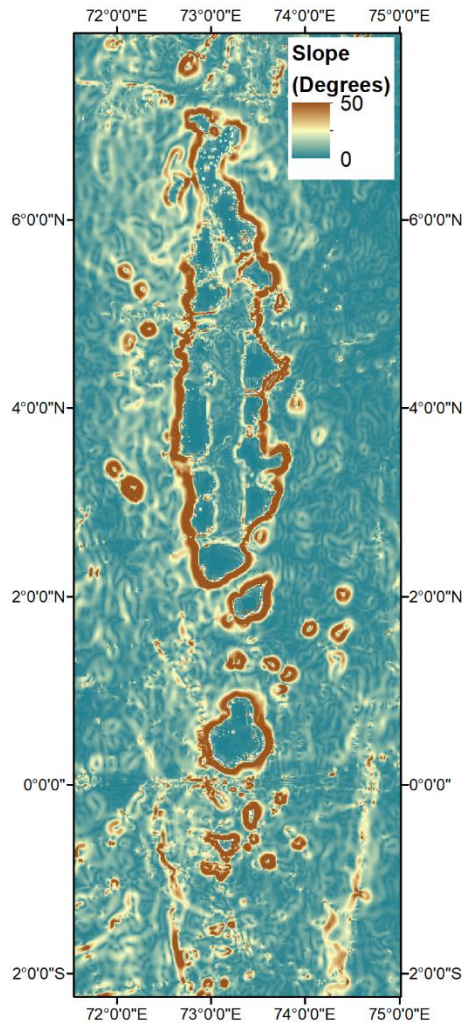
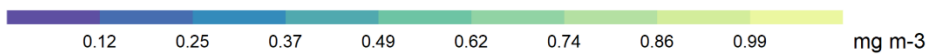
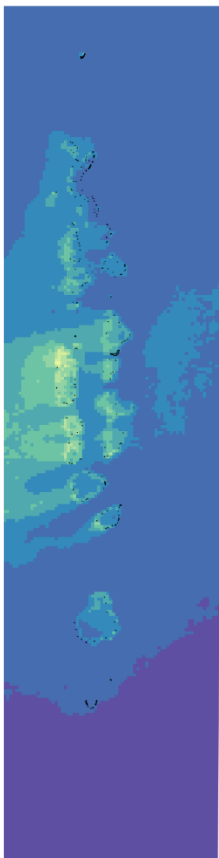


Figure S1. Values of seafloor slope, or gradient, measured in degrees from 0-90 across the Maldives archipelago.

Average Monthly chlorophyll-a



(a) 01-2019



(b) 08-2019



Figure S2. Sample of monthly chlorophyll-a concentrations (mg/m³) in (a) January 2019 (LHS) and (b) August 2019 (RHS) across the wider Maldivian archipelago from 3°S to 9°N and 72°E to 75°E. January is a Northeast (NE) monsoon month and August is a Southwest (SW) monsoon month.

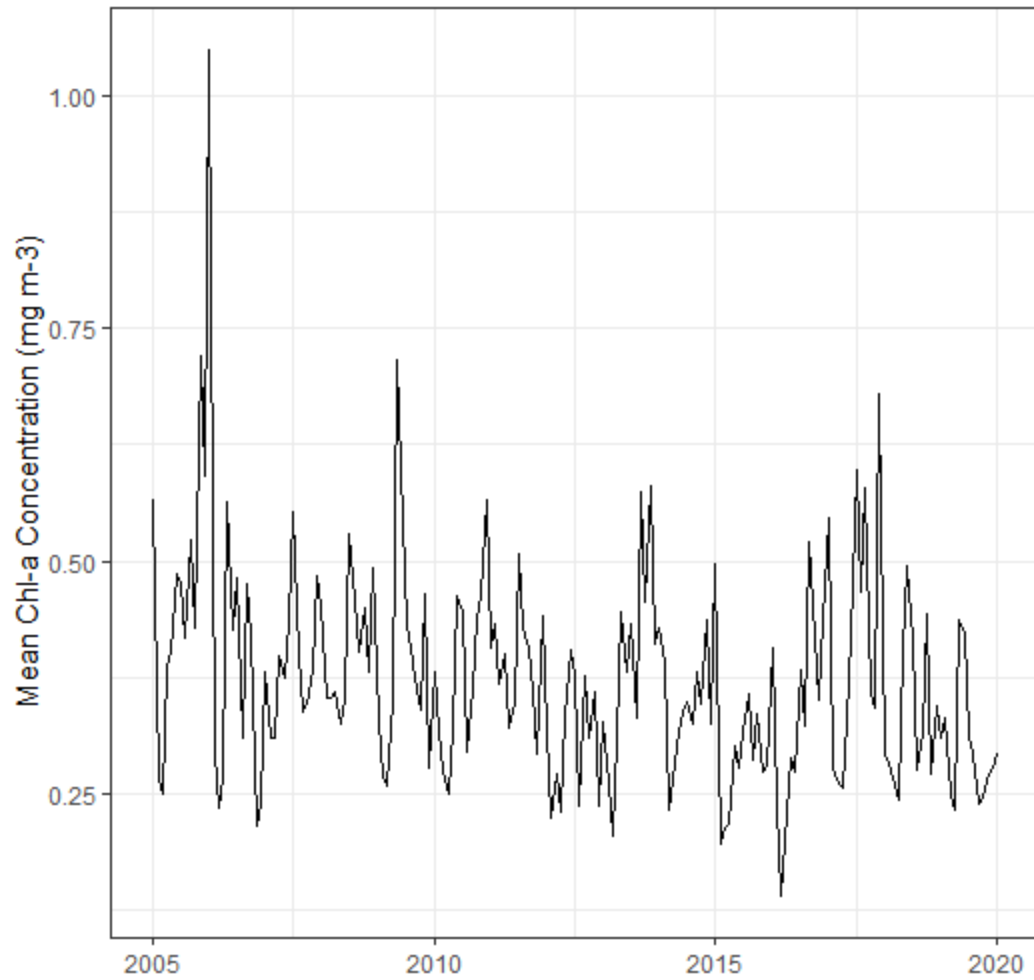


Figure S3. Time-series of variation in monthly mean chlorophyll-a concentration (mg/m^3) in the 4km by 4km grid cell for Male City, North Male Atoll, in the central Maldives (Jan 2005 – Dec 2019).

Average monthly sea surface temperature

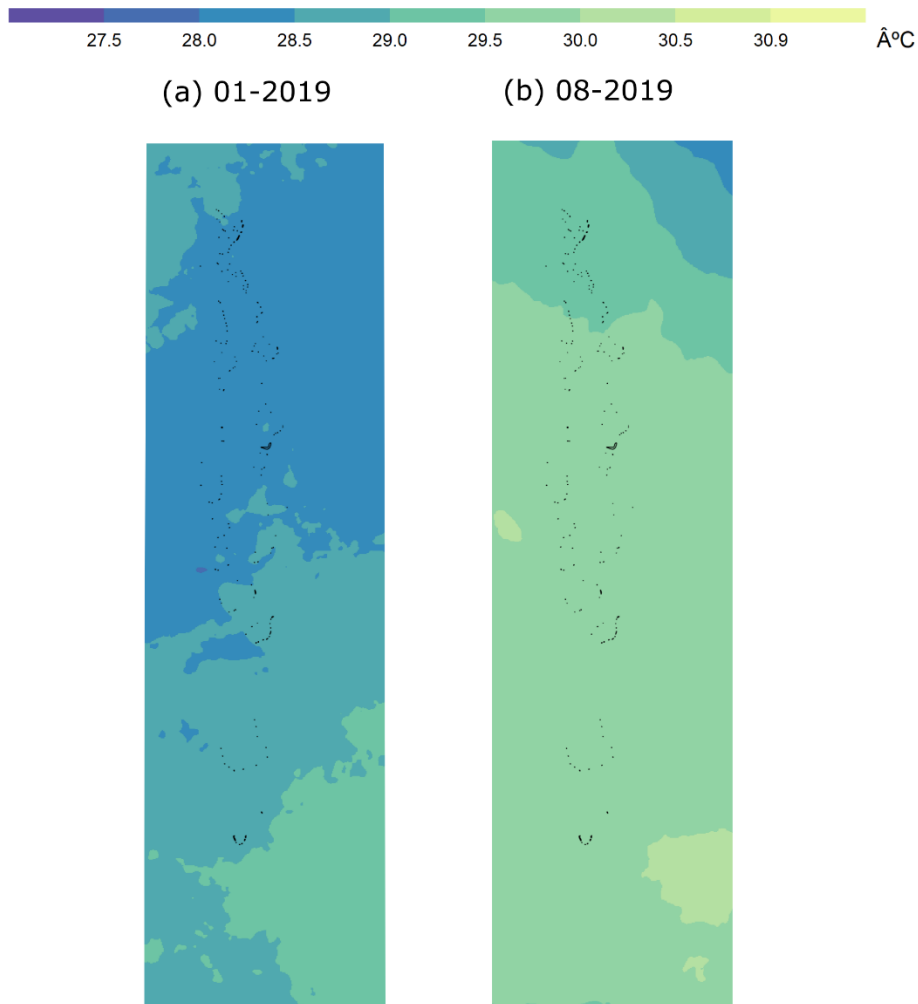


Figure S4. Sample of monthly sea surface temperature (sst) (°C) in (a) January 2019 (LHS) and (b) August 2019 (RHS) across the wider Maldivian archipelago from 3°S to 9°N and 72°E to 75°E. January is a Northeast (NE) monsoon month and August is a Southwest (SW) monsoon month.

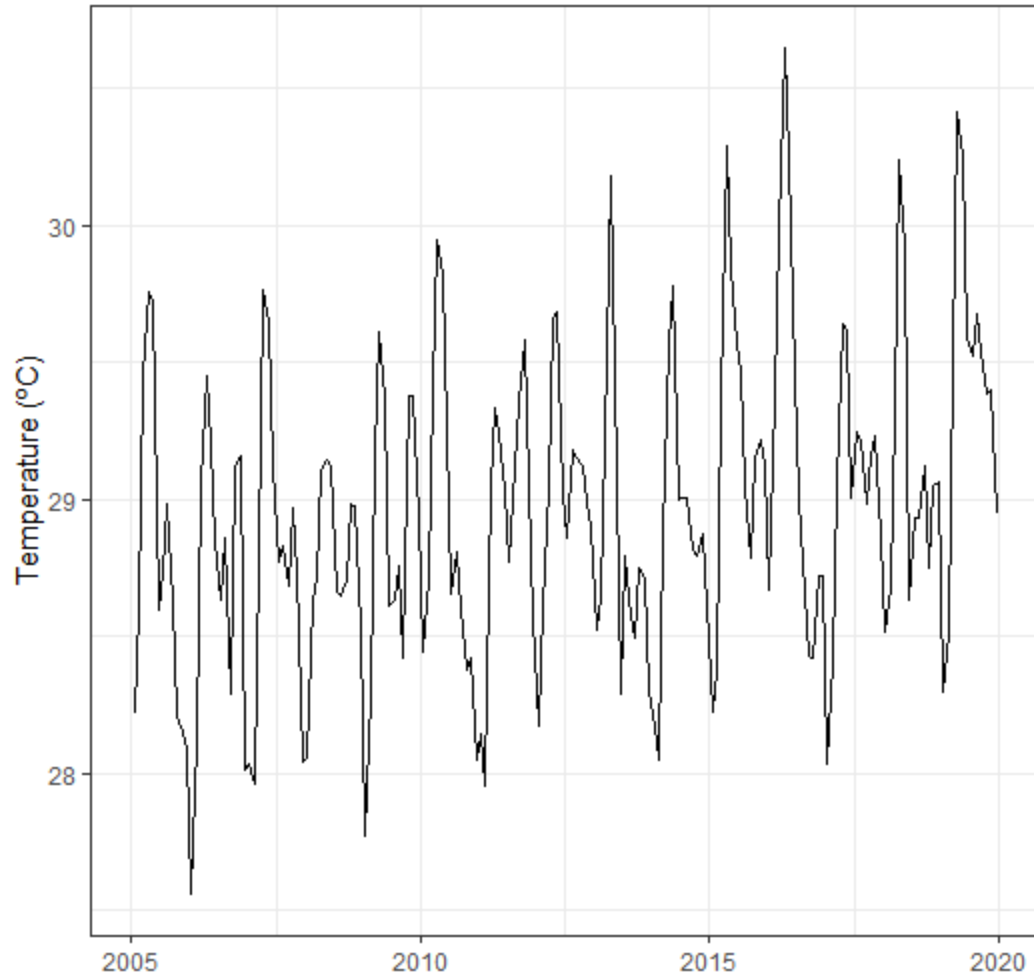


Figure S5. Time-series of variation in monthly mean sea surface temperature (°C) in the approximately 1.1km by 1.1 km grid cell for Male City, North Male Atoll, in the central Maldives (Jan 2005 – Dec 2019).

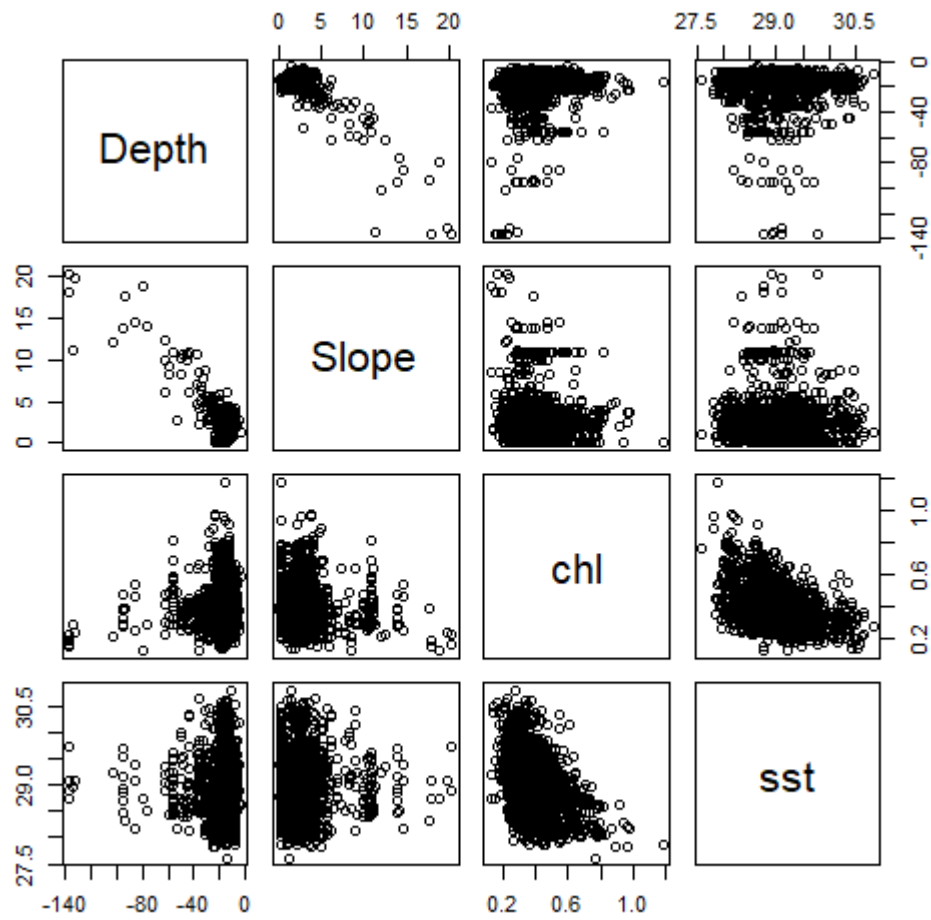


Figure S6. Plots of relationships between environmental variables used to check for collinearity. Plots show environmental variables extracted for sites and days where sightings of feeding reef manta rays were recorded.

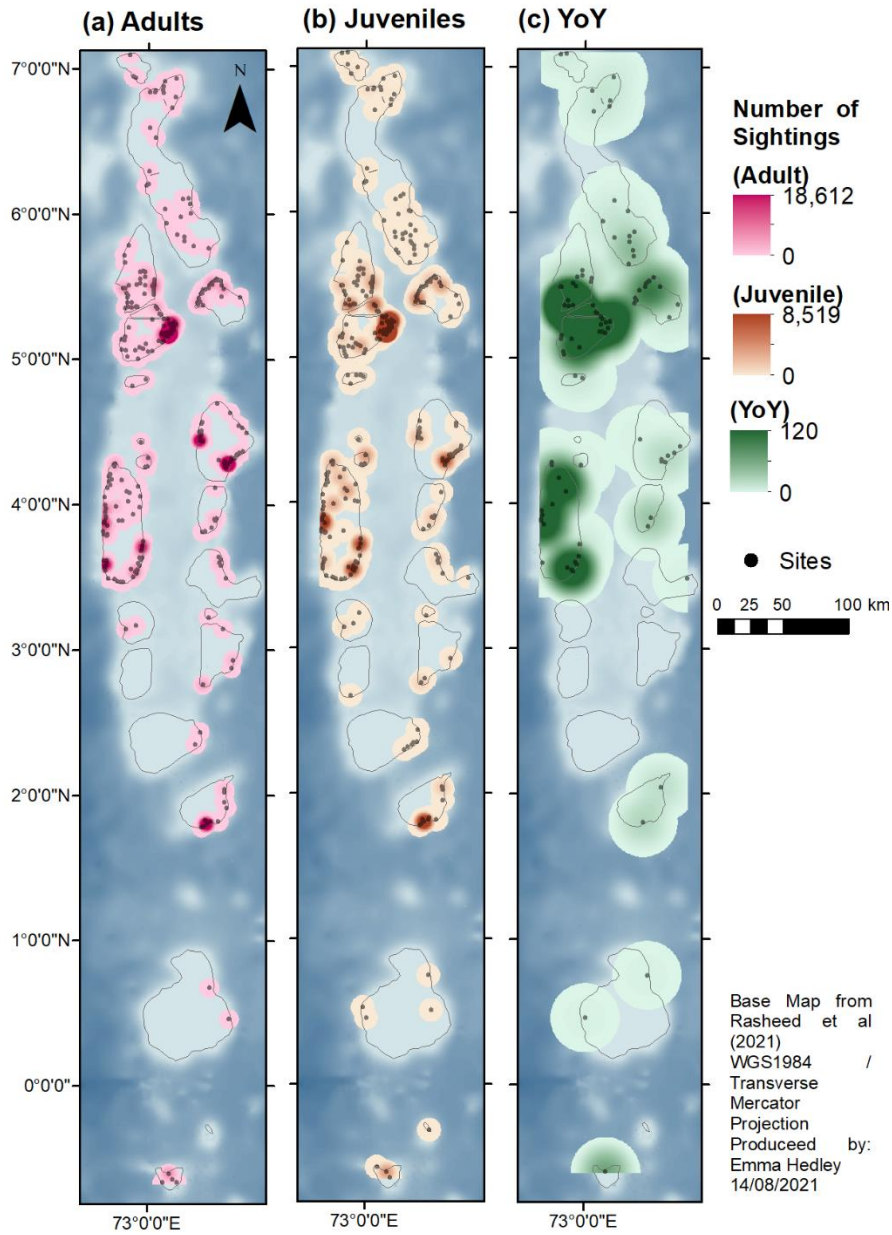


Figure S7. Heatmap representing total number of reef manta ray sightings of (a) adult, (b) juvenile, and (c) young of year (YoY) individuals across the Maldivian archipelago (1987-2019). Darker shades of colour indicate areas with higher numbers of sightings.

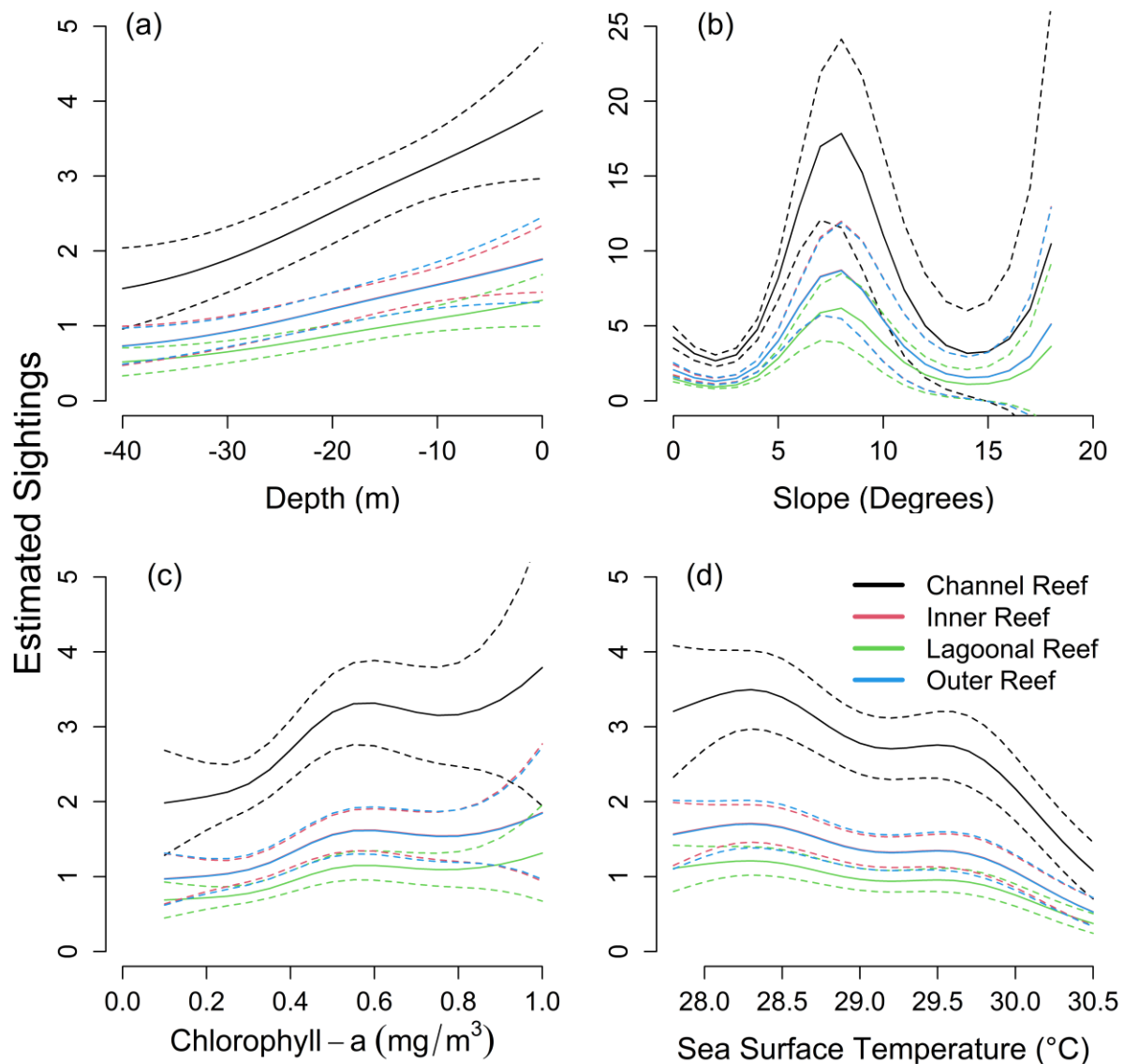


Figure S8. Estimated number of sightings of adult reef manta rays during the NE monsoon season displaying feeding behaviour on days when manta rays were sighted with changing values of (a) depth, (b) slope, (c) chlorophyll-a concentration, and (d) sea surface temperature with each other co-variate held at its mean value. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of estimated sightings for channel reefs followed by inner reefs, outer reefs, and lagoonal reefs.

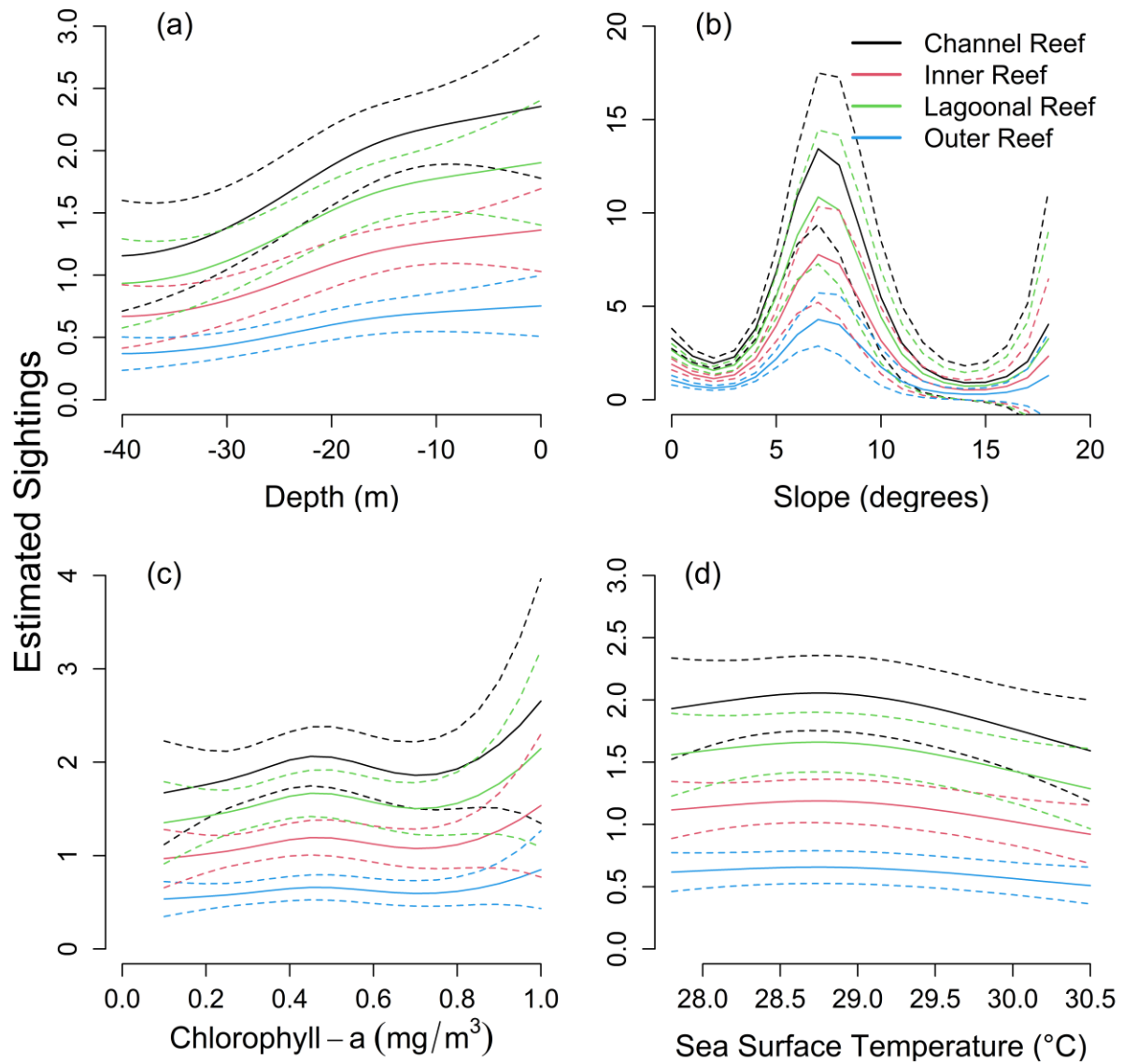


Figure S9. Estimated number of sightings of juvenile reef manta rays during the NE monsoon season displaying feeding behaviour on days when manta rays were sighted with changing values of (a) depth, (b) slope, (c) chlorophyll-a concentration, and (d) sea surface temperature with each other co-variate held at its mean value. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of estimated sightings for channel reefs followed by inner reefs, outer reefs, and lagoonal reefs.

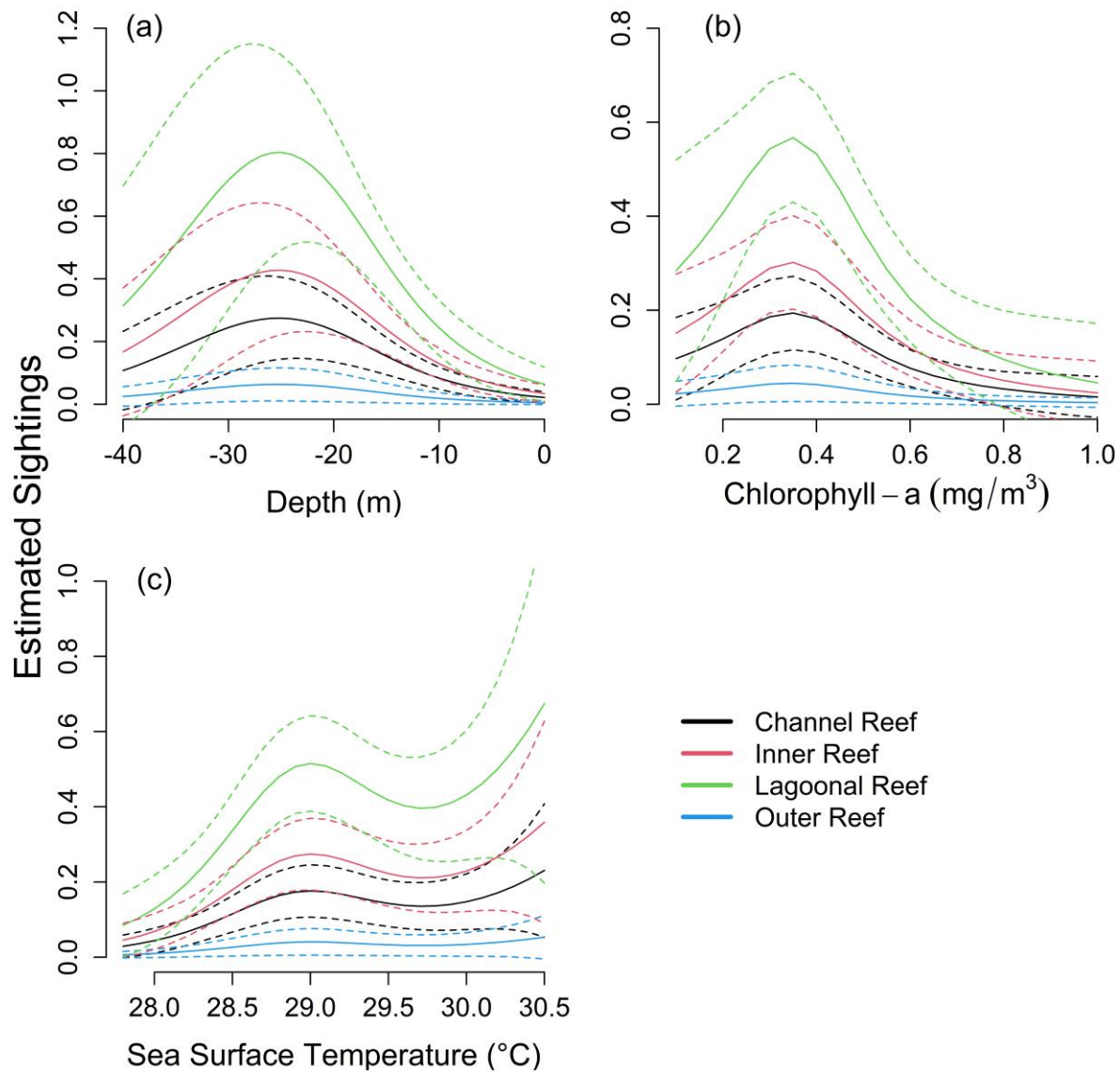


Figure S10. Estimated number of sightings of young of year (YoY) reef manta rays during the NE monsoon season displaying feeding behaviour on days when manta rays were sighted with changing values of (a) depth, (b) slope, (c) chlorophyll-a concentration, and (d) sea surface temperature with each other co-variate held at its mean value. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of estimated sightings for channel reefs followed by inner reefs, outer reefs, and lagoonal reefs.

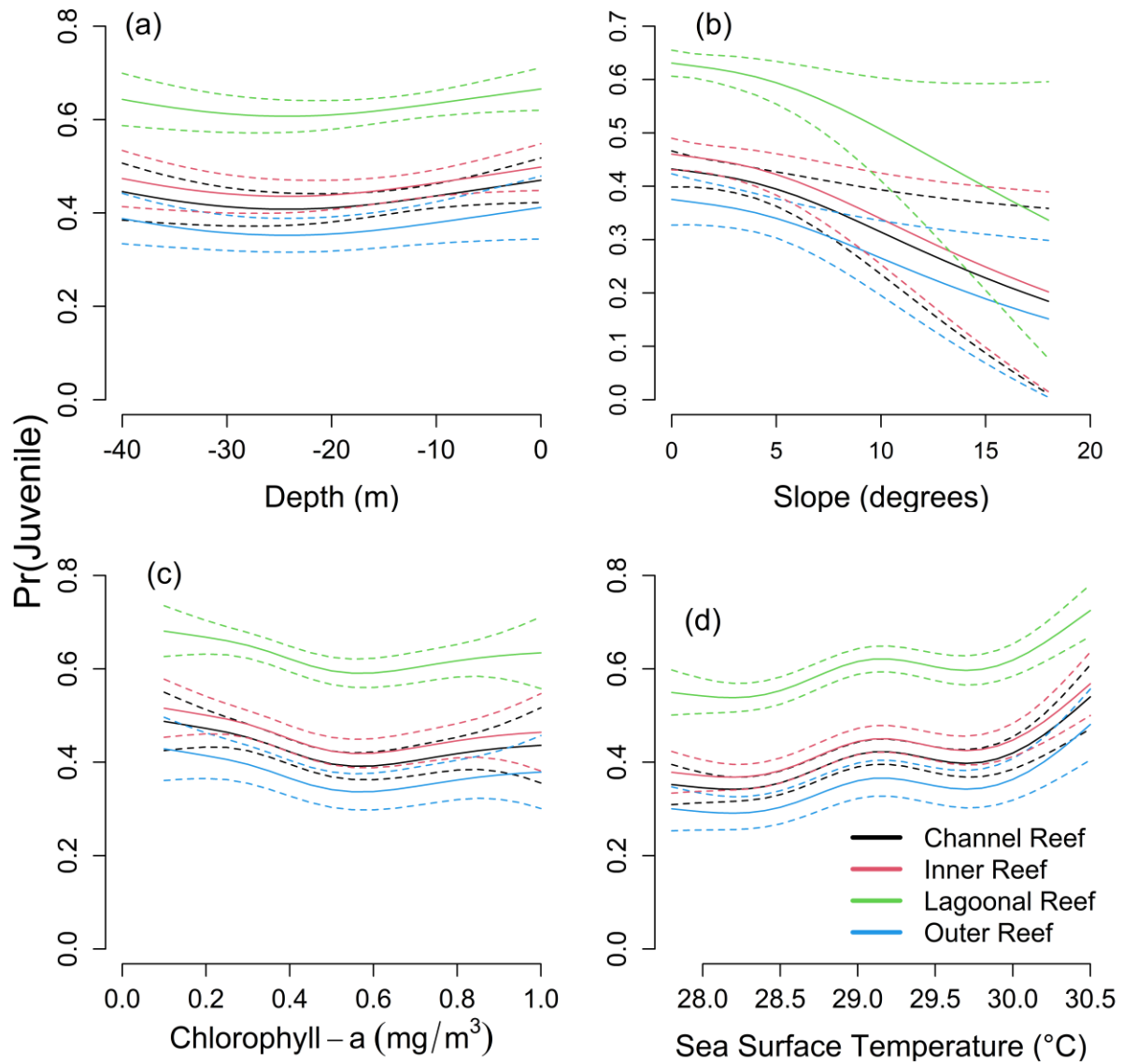


Figure S11. Estimated probability of a sighting of a feeding reef manta ray being a juvenile ($Pr(juv)$) during the NE monsoon with changing values of (a) depth, (b) slope, (c) chlorophyll-a and (d) sea surface temperature, and all other co-variables held at their mean values. Coloured lines representing reef type, with 95% confidence intervals, show the highest numbers of predicted sightings for lagoonal reefs followed by inner reefs, channel reefs, and outer reefs.

Table S1. Estimated (est.) seasonal sightings and mean observed (obs.) sightings during the SW monsoon for adult, juvenile, and YoY reef manta rays (2005-2019).

Location			Adult		Juvenile		YoY	
Site	Latitude	Longitude	Est.	Obs.	Est.	Obs.	Est.	Obs.
Aidhoo Beyru	5.1842	73.1681	9.2	0.5	5.4	0.5	0.0	0.0
Alidhuffarufinolhu Faru	6.8557	73.1009	0.5	1.0	0.9	1.0	0.1	0.0
Andhagiri	5.2220	73.1635	4.5	5.1	2.3	3.5	0.0	0.0
Angafaru	5.1753	73.0977	4.1	5.0	2.7	2.5	0.1	0.0
Angafaru Falhu	5.1803	73.1027	2.2	37.0	3.0	25.5	0.1	1.0
Arilundhoo Faru	5.6590	72.9594	2.9	0.0	2.0	1.0	0.1	0.0
Bathalaa Faru	5.3496	73.0691	6.1	6.0	4.7	3.6	0.1	0.0
Bathalaa Kanduu	5.3618	73.0599	8.6	3.2	4.3	7.0	0.0	0.0
Bodu Lhaimendhoo	6.0033	73.3079	2.4	0.0	1.7	1.0	0.0	0.0
Bodu Thila	5.1688	73.1306	8.5	10.5	5.2	2.5	0.1	0.0
Boduhithi Thila	4.4508	73.3623	0.8	5.5	1.2	2.0	0.1	0.0
Boduhuraa Beyru	1.7748	73.3789	0.8	1.0	0.1	0.0	0.0	0.0
Boomerang Faru	5.5137	72.9234	0.6	1.3	0.9	1.3	0.1	0.0
Christmas Rock	5.8140	73.2532	0.9	1.0	0.9	0.0	0.1	0.0
Cliffhanger	3.1669	72.9249	3.9	1.0	3.0	0.0	0.1	0.0
Dhandhoo Diner	5.2137	73.1824	3.6	1.7	2.3	0.8	0.1	0.0
Dhandhoo Falhu	5.2250	73.1793	3.2	3.0	2.3	3.7	0.1	0.0
Dhangethi Beyru	3.5796	72.9509	6.5	0.0	2.8	2.0	0.0	1.0
Dhangethi Falhu	3.5930	72.9400	4.4	0.8	3.1	2.0	0.1	0.5
Dhanifaru	5.3981	73.3562	0.9	0.6	1.3	1.6	0.1	0.0
Dharavandhoo Corner	5.1558	73.1420	7.6	4.6	3.1	1.9	0.0	0.0
Dharavandhoo Thila	5.1610	73.1228	3.4	1.0	2.3	0.0	0.1	0.0
Dhidhdhoo Beyru	5.3731	73.3836	1.2	0.3	0.9	1.0	0.0	0.0
Dhidhdhoo Finolhu Beyru	3.5000	72.9054	3.7	0.0	1.4	1.0	0.0	0.0
Dhiggaru Kanduu	3.7151	72.9709	7.5	7.7	4.2	3.4	0.0	0.0
Dhiggiri Faru	3.6421	73.4908	9.9	4.0	5.5	2.0	0.0	0.0
Dhigu Thila	5.1743	73.1080	4.1	7.7	2.2	1.7	0.1	0.0
Dhigurah Beyru	3.5271	72.9281	3.3	1.0	1.3	0.2	0.0	0.2
Dhigurah Falhu	3.5359	72.9183	2.0	1.4	2.9	2.4	0.1	0.1
Dhikkuredhdhoo Finolhu	5.5697	72.9854	3.3	8.7	2.1	5.0	0.1	0.3
Dhiya Adi Kanduu	4.5466	73.6262	18.6	1.0	13.3	0.0	0.1	0.0
Dhonfanu Faru	5.1832	73.1243	4.7	10.2	2.6	3.3	0.0	0.0
Dhonfanu Thila	5.1720	73.1161	3.6	12.5	2.7	6.0	0.1	0.0
Dhunikulhu Faru	5.0406	72.8557	0.6	0.0	0.9	2.0	0.2	0.0
Dhunikulhu Kanduu	5.0043	72.8726	4.3	0.0	6.3	1.0	0.0	0.0
Dhuvan Faru	3.5533	72.8890	4.3	1.3	2.7	1.9	0.0	0.0

Ellaidhoo Faru	4.0056	72.9515	3.8	0.0	2.4	1.0	0.1	0.0
Fahala Beyru	2.4331	73.3652	0.7	1.0	0.0	0.0	0.0	0.0
Felivaru Thila	5.4690	73.3773	0.9	0.5	1.1	0.5	0.1	0.3
Fenfushi Beyru	3.4837	72.7800	2.3	1.0	2.1	0.5	0.0	0.0
Fesdu Falhu	3.9893	72.7865	0.6	0.7	1.6	1.5	0.2	0.0
Finolhoss Faru	5.2312	73.1125	4.1	0.5	2.8	0.5	0.1	0.5
Fulhadhoo Falhu	4.8756	72.9369	2.2	0.0	2.0	1.0	0.1	1.0
Fushi Kandu	2.0386	73.5326	7.6	2.2	4.5	1.3	0.0	0.0
Fushifaru Kandu	5.4904	73.5220	7.8	1.6	4.5	1.8	0.0	0.2
Gaakoshinbi Faru	6.2951	73.0081	2.7	2.0	2.1	0.0	0.0	0.0
Gaamadhoo	4.3048	73.5798	10.1	0.0	4.9	1.0	0.0	0.0
Gan Beyru	1.9115	73.5481	5.8	1.0	2.5	0.0	0.0	0.0
Gangehi Falhu	4.2601	72.7777	0.6	0.8	1.9	2.0	0.3	0.2
Gasfinolhu Beyru	4.3560	73.6352	2.6	2.0	2.0	1.2	0.0	0.0
Gasgandufinolhu Faru	1.9492	73.5350	2.8	1.0	2.1	0.0	0.1	0.0
Gemanaa Giri	5.5259	72.9487	3.3	2.0	2.4	2.0	0.1	0.0
Genburugau Falhu	4.1700	72.8272	0.7	0.5	2.1	1.4	0.3	0.3
Goidhoo Falhu	4.8622	72.9891	3.6	0.0	2.4	1.0	0.0	1.0
Guraidhoo Falhu	3.8984	73.4611	7.4	1.1	4.4	1.2	0.0	0.1
Guraidhoo Kandu S-M	3.8921	73.4701	32.3	1.0	19.7	0.0	0.1	0.0
Guraidhoo Kandu Thaa	2.3294	73.3281	4.6	0.0	2.9	1.0	0.1	0.0
Hani Kandu	5.4143	73.3500	3.0	0.0	4.2	1.0	0.1	0.0
Hanifaru Bay	5.1731	73.1462	15.9	21.1	7.9	9.6	0.0	0.0
Hanifaru Beyru	5.1752	73.1610	7.2	12.3	1.8	3.0	0.0	0.0
Hanifaru Falhu	5.1774	73.1461	2.8	7.0	3.9	6.0	0.2	0.0
Hanifaru Faru	5.1811	73.1302	10.4	5.7	4.3	1.3	0.0	0.0
Hinnavaru Faru	5.4919	73.4183	2.3	0.0	2.1	1.0	0.0	1.0
Hithadhoo Corner	1.7983	73.4100	3.6	2.0	1.5	0.5	0.0	0.0
Hoandedhdhoo Faru	0.4497	73.0139	0.5	0.0	0.7	1.0	0.1	1.0
Hudhuveli Beyru	4.2928	73.5688	10.1	1.0	7.8	0.0	0.0	0.0
Hulhimendhoo Corner	1.8150	73.3972	0.5	0.0	0.8	1.0	0.1	0.0
Hurai Faru	5.2072	73.1619	9.2	5.8	4.9	2.5	0.0	0.0
Hurai Thila	5.2006	73.1824	9.1	1.3	6.1	1.3	0.0	0.0
Huravalhi Falhu	3.6875	72.9627	8.1	3.8	4.3	1.4	0.0	0.0
Huravalhi Finolhu	5.5252	73.4391	0.9	1.0	1.1	0.9	0.1	0.0
Iguraidhoo Beyru	5.4757	73.0446	5.7	2.0	2.1	2.0	0.0	0.0
Innamaadhoo Beyru	5.5496	73.0493	5.6	9.0	2.3	8.0	0.0	1.0
Kabaalifaru	6.1200	73.2581	5.3	0.0	2.4	1.0	0.0	0.0
Kalhudheyfushi Faru	2.2979	73.2734	2.1	0.0	1.8	1.0	0.0	0.0
Kamadhoo Faru	5.2819	73.1424	39.1	7.3	15.4	1.7	0.0	0.0
Kandolhu Maaha	4.0217	72.8701	5.0	2.0	3.7	0.0	0.1	0.0
Kandooma Thila	3.9074	73.4776	9.3	0.0	5.7	0.0	0.0	0.0

Kani Corner	4.3406	73.6136	13.3	1.5	4.7	1.1	0.0	0.0
Kanifushi Falhu	5.3806	73.3454	1.2	2.8	1.3	3.8	0.1	0.5
Kottefaru Beyru	5.5135	73.0482	7.0	6.7	2.9	2.3	0.0	0.0
Kottefaru Thila	5.5231	73.0448	4.0	8.2	2.3	4.3	0.1	0.1
Kuda Huraa Faru	4.3276	73.5926	4.4	0.0	2.5	1.0	0.0	0.0
Kuda Lhaimendhoo	6.0103	73.2963	3.0	1.0	1.2	1.0	0.0	0.0
Kudadhoo Faru	5.0519	73.0024	7.7	1.0	3.0	2.0	0.0	0.0
Kudadhoo Kanduu	5.5108	73.4231	2.3	1.0	2.2	1.5	0.0	0.5
Kudahaiykodi Faru	5.6031	72.9853	3.9	9.1	2.6	6.1	0.1	0.1
Kukulhudhoo Corner Raa	5.4543	72.8553	1.3	1.0	1.7	0.0	0.1	0.0
Kuramathi Faru	4.2618	72.9775	3.5	0.0	1.3	1.0	0.0	1.0
Kuredu Caves Express	5.5556	73.4759	1.7	0.2	1.8	1.4	0.1	0.0
Kuredu Faru	5.5453	73.4664	1.1	0.5	1.1	1.3	0.0	0.0
Landaa Giraavaru Faru	5.2828	73.1133	8.0	3.0	5.3	1.3	0.1	0.0
Lankan Beyru	4.2804	73.5569	5.2	1.3	1.2	0.0	0.0	0.0
Lhohifushi Aquarium	4.3470	73.6220	19.4	0.7	7.2	1.2	0.0	0.0
Maa Faru Falhu	5.1321	72.8415	0.4	1.0	1.6	2.2	0.3	0.0
Maabaidhoo Kanduu	2.0201	73.5341	11.7	0.0	7.3	1.0	0.0	0.0
Maalifushi Faru	2.3147	73.2965	2.0	0.0	1.7	1.0	0.1	0.0
Maamigili Beyru	3.4674	72.8390	3.3	2.0	1.4	0.0	0.0	0.0
Maaneigaa	5.0744	72.9683	0.7	1.0	2.1	2.9	0.3	0.6
Maarogaali	5.0820	72.9478	0.8	0.3	2.1	2.5	0.3	0.0
Maavaru Beyru Baa	5.1373	72.8234	0.7	0.0	1.3	1.0	0.0	0.0
Maavaru Falhu	3.8539	72.7275	0.8	1.0	2.3	1.9	0.2	0.3
Maavaru Kanduu Baa	5.1553	72.8464	3.7	1.5	5.2	3.5	0.1	0.0
Maayafushi Falhu	4.0793	72.8791	2.8	0.0	3.8	1.6	0.1	0.3
Madifushi Faru	2.3474	73.3355	2.8	0.0	2.0	1.0	0.1	0.0
Madivaafaru Faru	5.6106	72.9670	3.1	2.0	2.1	5.0	0.0	0.0
Mahibadhoo Thila	5.5578	72.9528	4.1	0.0	2.9	1.0	0.1	1.0
Mahidhoo Faru	5.5572	72.9475	3.2	10.3	2.1	8.7	0.1	0.0
Manafaru	6.9922	72.9414	3.5	0.0	2.1	1.7	0.1	0.0
Mathidhoo Beyru	2.3486	73.3581	2.8	0.0	2.1	1.0	0.0	0.0
Medhafushi Faru	5.7428	73.3324	1.5	0.0	1.8	1.0	0.1	1.0
Medhu Kanduu	3.6181	73.5051	8.0	1.5	4.1	0.5	0.0	0.0
Mendhoo Beyru	1.7843	73.3912	2.0	2.0	1.5	1.0	0.0	0.0
Miyaru Kanduu	3.5981	73.4987	9.1	1.8	4.5	1.0	0.0	0.0
Moofushi Bojamhadi	3.8764	72.7064	1.1	0.0	1.4	1.0	0.0	0.0
Moofushi Denagili	3.8857	72.7080	1.4	0.0	1.3	1.0	0.0	1.0
Mulikolhu Faru	-0.6500	73.1760	5.2	1.0	4.1	0.0	0.1	0.0
Muravandhoo Faru	5.6058	72.9492	3.4	0.5	2.2	0.5	0.0	0.0
Muravandhoo Thila	5.6022	72.9580	4.8	0.0	3.2	2.0	0.1	0.0
Nagili Falhu	5.0954	72.9324	0.7	0.0	1.5	1.0	0.1	0.0

Nalaguraidhoo Beyru	3.4723	72.7988	0.5	0.0	0.9	1.0	0.0	0.0
Nelivaru Beyru	5.1206	73.1019	8.0	3.0	3.4	0.0	0.0	0.0
Neyo Beyru	5.4923	73.0431	7.7	13.0	3.2	4.5	0.0	0.0
Okalhu Thila	3.6809	72.9586	4.5	9.0	3.0	1.0	0.1	0.0
Olhuveli Falhu	3.8392	73.4425	6.9	0.0	3.8	1.0	0.0	0.0
Olhuveli Faru	1.8238	73.4031	0.6	1.0	0.9	0.0	0.1	0.0
Orivaru Giri	5.7998	73.3097	1.7	0.0	2.2	2.0	0.1	2.0
Radhdhiggaa Falhu	3.7571	72.7638	1.6	0.0	1.8	1.0	0.1	0.0
Randheli Falhu	5.7041	73.3376	3.0	0.0	2.2	1.3	0.1	1.0
Rangali Falhu	3.6128	72.7245	0.8	0.0	2.2	1.0	0.1	0.0
Rannalhi Falhu	3.9214	73.3646	1.2	0.0	1.6	0.0	0.1	0.0
Ranveli Kandu	3.6203	72.9617	7.7	1.0	4.0	0.0	0.0	0.0
Rasdhoo Madivaru	4.2635	72.9997	12.1	2.0	8.2	0.0	0.1	0.0
Reethi Falhu	5.2524	73.1768	2.7	3.4	3.8	3.4	0.2	0.1
Rihiveli Falhu	3.8143	73.3997	0.6	1.0	1.6	0.0	0.1	0.0
Sunlight Faru	4.3003	73.5337	5.5	3.3	3.4	0.7	0.1	0.0
Thanburudhoo Faru	4.3256	73.5789	3.1	0.5	2.1	0.5	0.1	0.5
Thanburudhoo Kandu	5.7172	73.2274	1.5	0.0	2.0	1.0	0.1	0.0
Thiladhoo Faru	5.2557	73.1797	3.0	0.5	2.1	1.5	0.1	0.0
Three Rocks	5.3969	73.3607	0.7	0.0	1.1	1.0	0.2	0.0
Thulusdhoo Beyru	4.3687	73.6560	5.9	1.0	1.9	0.5	0.0	0.0
Thundufushi Falhu	3.7853	72.7250	0.6	0.0	1.6	1.0	0.1	0.0
Ukulhas Faru	4.2246	72.8584	2.9	0.0	2.1	1.0	0.1	0.0
Uthurumaafaru Kandu	5.6654	72.8459	2.0	1.0	1.9	3.0	0.0	0.0
Vandhoomaa Beyru	5.2408	73.1957	10.9	4.0	4.3	3.1	0.0	0.0
Vattaru Kandu	3.2210	73.4238	1.3	0.0	1.1	0.0	0.0	0.0
Veligandu Kandu	4.3227	73.0064	5.4	1.0	3.4	2.0	0.0	0.0
Veyofushi Falhu	5.2456	73.1494	3.1	2.6	3.5	3.5	0.1	0.0
Veyvah Faru	5.4344	73.3600	1.2	0.0	1.2	1.5	0.1	0.0
Vihamaafaru Falhu	4.1344	72.7459	1.5	1.0	1.9	1.0	0.1	0.0
Vilamendhoo Thila	3.6334	72.9670	7.1	7.7	3.9	4.0	0.1	0.0
Viligili Kandu Addu	-0.6721	73.2084	1.8	1.0	0.1	0.0	0.0	0.0
Viligilimathidhahuraa Falhu	4.3895	73.6614	3.9	0.0	4.1	1.0	0.0	0.5
Vinaneiy Faru	5.2411	73.1537	4.3	0.0	4.4	0.0	0.1	0.0
Vinaneiy Finolhu	5.3112	73.0904	6.5	1.0	3.2	0.0	0.1	0.0

Table S2. Estimated (est.) seasonal sightings and mean observed (obs.) sightings during the NE monsoon for adult, juvenile, and YoY reef manta rays (2005-2019).

Location			Adult		Juvenile		YoY	
Site	Latitude	Longitude	Est.	Obs.	Est.	Obs.	Est.	Obs.
Alidhuffarufinolhu Faru	6.8557	73.1009	1.2	1.0	1.1	0.4	0.3	0.0
Aliha Giri	5.4114	73.5289	1.0	0.0	0.9	0.0	0.1	0.0
Anemone Thila	5.4323	73.5099	1.2	4.0	1.0	0.0	0.1	0.0
Athurugau Faru	3.8885	72.8051	1.5	1.0	1.2	0.0	0.2	0.0
Bathalaa Kandu	5.3618	73.0599	3.0	1.0	1.9	3.0	0.0	0.0
Bodufinolhu Beyru	3.4913	72.7358	5.2	1.0	4.1	0.0	0.0	0.0
Boduhithi Faru	4.4377	73.3857	2.3	1.5	1.2	1.0	0.0	0.5
Boduhithi Thila	4.4508	73.3623	3.0	2.4	1.7	0.5	0.1	0.0
Boduhuraa Beyru	1.7748	73.3789	1.5	5.0	0.1	1.0	0.0	0.0
Boomerang Faru	5.5137	72.9234	1.2	3.1	1.1	1.6	0.2	0.2
Dhangethi Falhu	3.5930	72.9400	1.3	0.0	1.4	0.5	0.2	0.5
Dhanifaru	5.3981	73.3562	1.9	1.3	1.5	2.6	0.2	0.1
Dhidhdhoo Beyru	5.3731	73.3836	1.7	0.7	0.8	0.7	0.0	0.0
Dhiggaru Kandu	3.7151	72.9709	2.7	2.0	2.0	0.0	0.1	0.0
Dhigurah Beyru	3.5271	72.9281	1.0	0.5	0.6	0.5	0.0	0.0
Dhigurah Falhu	3.5359	72.9183	0.8	1.4	1.4	1.6	0.3	0.1
Dhonakulhi Kandu	6.8410	73.0487	3.0	0.8	2.1	0.8	0.0	0.3
Dhonakulhi North	6.8535	73.0537	1.6	1.0	0.8	1.3	0.0	0.0
Dhonkalo Thila	3.9714	72.7173	2.0	0.0	1.5	3.0	0.0	0.0
Dhuvan Faru	3.5533	72.8890	1.4	1.0	1.2	0.5	0.1	0.5
Eboodhoo Faru	5.0643	72.8511	2.3	2.0	1.3	2.0	0.0	0.0
Ellaidhoo Faru	4.0056	72.9515	0.9	0.0	1.0	1.0	0.2	0.0
Ellaidhoo Giri	4.0083	72.9341	1.5	0.0	1.0	1.0	0.1	0.0
Falhumaafushi Faru	0.6690	73.4321	0.8	0.0	0.8	0.0	0.2	0.0
Fehendhoo Falhu	4.8722	72.9699	1.2	0.0	1.1	1.0	0.1	0.0
Felivaru Beyru	5.4815	73.3818	1.7	1.0	0.9	1.0	0.1	0.0
Felivaru Faru	5.8382	73.3080	1.0	0.0	1.0	1.0	0.1	1.0
Felivaru Kandu	5.4846	73.3957	3.2	2.0	2.0	0.5	0.1	0.0
Felivaru Thila	5.4690	73.3773	1.4	2.4	1.2	0.7	0.1	0.0
Fenfushi Beyru	3.4837	72.7800	5.2	1.0	2.6	0.7	0.0	0.0
Fenfushi Beyru Raa	5.3939	72.8613	4.6	1.0	2.3	0.0	0.0	0.0
Fenfushi Faru	5.3950	72.8897	1.2	0.5	1.2	1.0	0.3	0.5
Fesdu Falhu	3.9893	72.7865	1.3	0.9	1.9	0.8	0.3	0.0
Fodhdhoo Beyru	5.7396	73.2126	2.9	0.0	1.2	2.0	0.0	0.0
Fonadhoo Beyru	1.8145	73.4922	1.3	3.5	0.6	0.8	0.0	0.0
Fotteyo Finolhu Faru	3.4818	73.7089	0.9	0.0	0.9	1.0	0.1	1.0

Fulhadhoo Falhu	4.8756	72.9369	0.9	0.0	0.9	1.0	0.1	1.0
Fushifaru Kandu	5.4904	73.5220	2.5	3.3	1.9	1.0	0.1	0.0
Fushivelavaru Faru	5.8282	73.2044	0.9	0.0	0.9	1.0	0.2	1.0
Gaadhoo Beyru	1.8143	73.4402	3.6	1.7	3.8	1.3	0.2	0.0
Gaakoshinbi Faru	6.2951	73.0081	1.2	4.0	1.1	0.0	0.1	0.0
Gangehi Beyru	4.2771	72.7715	1.8	1.6	0.7	0.8	0.0	0.0
Gangehi Falhu	4.2601	72.7777	1.5	1.7	2.4	1.6	0.5	0.0
Genburugau Falhu	4.1700	72.8272	1.6	0.4	2.5	1.5	0.5	0.3
Guraidhoo Falhu	3.8984	73.4611	1.5	0.0	1.7	1.0	0.1	0.0
Guraidhoo Kandu S-M	3.8921	73.4701	6.6	1.0	6.9	0.0	0.1	0.0
Guraidhoo Kandu Thaa	2.3294	73.3281	1.4	0.0	1.3	1.0	0.1	0.0
Haafushi Falhu	2.7857	73.4137	1.1	0.0	1.8	1.0	0.2	0.0
Hadahaa Faru	0.5028	73.4572	0.9	0.0	0.8	1.0	0.1	0.0
Hani Kandu	5.4143	73.3500	10.2	1.5	6.1	0.3	0.2	0.0
Hanifaru Bay	5.1731	73.1462	5.1	19.0	3.5	7.3	0.1	0.0
Hembadhoo Thila	4.4826	73.3753	3.4	6.0	2.6	3.0	0.1	0.0
Himendhoo Thila	3.9159	72.7178	3.9	3.0	2.0	0.0	0.0	0.0
Hinnavaru Faru	5.4919	73.4183	3.1	2.0	2.1	0.0	0.1	0.0
Hithadhoo Corner	1.7983	73.4100	1.1	0.9	0.8	0.7	0.0	0.0
Horubadhoo Faru	5.1624	73.0636	1.6	0.0	1.2	1.0	0.0	0.0
Hudhufushi Faru	5.3684	73.6427	1.0	0.0	1.0	1.0	0.1	1.0
Huivani Faru	5.9081	73.3093	1.2	0.0	1.1	1.0	0.1	0.0
Hukurudhoo Beyru	3.5706	72.7120	2.3	2.4	1.0	0.8	0.0	0.0
Huravalhi Faru	5.5190	73.4451	1.9	1.0	1.2	0.5	0.1	0.0
Huravalhi Finolhu	5.5252	73.4391	1.9	2.1	1.2	0.7	0.1	0.0
Huruelhi Beyru	3.5432	72.7144	1.2	1.0	0.7	1.0	0.0	0.0
Innafushi Faru	3.7973	72.7280	3.3	3.8	2.1	1.8	0.1	0.0
Kalhahandhi Huraa	3.7978	72.7047	1.9	2.2	0.7	0.5	0.0	0.0
Kandolhu Maaha	4.0217	72.8701	1.9	0.0	1.7	1.0	0.1	0.0
Kanifushi Falhu	5.3806	73.3454	1.6	1.9	1.3	1.7	0.2	0.1
Kelaa Falhu	6.9382	73.1947	1.2	2.3	2.4	1.3	0.3	0.7
Koathey Beyru	-0.5774	73.0866	5.4	0.0	7.8	1.0	0.0	0.0
Kuda Falhu	3.1413	72.8586	1.4	3.0	0.7	2.0	0.0	0.0
Kuda Kandu	4.4603	73.3640	2.6	1.0	2.1	1.0	0.2	0.0
Kuda Miyaru Thila	3.8023	72.8545	1.3	0.0	1.3	1.0	0.3	0.0
Kudadhoo Kandu	5.5108	73.4231	4.0	1.3	2.3	0.0	0.0	0.0
Kukulhudhoo Corner Raa	5.4543	72.8553	3.0	2.0	2.0	1.3	0.1	0.0
Kukulhudhoo Faru	5.4897	72.8456	3.6	1.0	2.1	2.0	0.1	1.5
Kurali Kandu	2.7585	73.3867	2.6	1.0	0.7	0.0	0.0	0.0
Kuramathi Beyru	4.2560	72.9851	2.3	0.4	1.3	0.8	0.0	0.0
Kuredhivaru Faru	5.8717	73.3438	1.1	0.0	1.0	1.0	0.1	1.0
Kuredu Caves Express	5.5556	73.4759	2.8	0.6	1.9	0.6	0.1	0.0

Kuredu Faru	5.5453	73.4664	1.6	0.8	1.1	0.6	0.1	0.0
Kuroshigiri Thila	5.5081	72.8696	1.4	1.0	1.2	0.0	0.2	0.0
Landaa Giraavaru Faru	5.2828	73.1133	2.2	1.2	2.2	1.1	0.1	0.2
Lankan Beyru	4.2804	73.5569	1.2	1.0	0.5	0.0	0.0	0.0
Maa Faru Beyru	5.4286	72.8625	2.1	1.7	0.8	0.7	0.0	0.0
Maa Faru Falhu	5.1321	72.8415	1.3	1.5	2.3	1.5	0.6	0.1
Maafinolhu Faru	7.0117	72.8707	1.2	0.0	1.1	1.0	0.2	0.0
Maalhoss Thila	3.9970	72.7147	3.6	1.0	1.7	0.0	0.0	0.0
Maamaduvvari West	5.0054	72.9361	1.0	1.0	0.8	0.0	0.0	0.0
Maamigili Beyru	3.4674	72.8390	1.3	1.4	0.7	0.2	0.0	0.0
Maamunagau Beyru	5.3530	72.8493	1.9	4.0	0.9	0.0	0.0	0.0
Maamunagau Falhu	5.3562	72.8933	1.0	3.5	1.7	8.5	0.5	2.6
Maamunagau Faru	5.3621	72.9206	3.3	0.3	2.9	5.7	0.3	1.0
Maamunagau Thila	5.3630	72.9288	3.1	1.0	2.7	1.0	0.2	0.0
Maaneigaa	5.0744	72.9683	1.3	0.5	2.2	2.0	0.6	0.0
Maarogaali	5.0820	72.9478	1.3	2.0	2.1	4.0	0.5	0.0
Maavaru Beyru Ari	3.8140	72.7016	2.4	2.3	0.8	1.4	0.0	0.0
Maavaru Beyru Baa	5.1373	72.8234	3.0	2.4	2.0	2.9	0.0	0.0
Maavaru Falhu	3.8539	72.7275	1.8	0.8	2.5	1.7	0.2	0.0
Maavaru Kandu Ari	4.2814	72.7808	2.7	1.5	1.4	1.0	0.1	0.0
Maavaru Kandu Baa	5.1553	72.8464	9.8	1.5	6.4	1.4	0.1	0.2
Maayafushi Falhu	4.0793	72.8791	1.0	0.1	1.8	1.7	0.3	0.1
Madi Thila	4.4740	73.3643	1.7	1.0	1.4	0.0	0.2	0.0
Madivaru Beyru	4.5064	73.3600	3.4	0.0	1.3	0.0	0.0	0.0
Madivaru Corner	4.4904	73.3705	3.6	3.6	2.5	0.6	0.1	0.0
Madivaru Faru	5.4593	73.3741	1.5	1.0	1.2	0.0	0.1	0.0
Madivaru Kandu	5.4541	73.3665	3.9	0.7	2.3	2.3	0.0	0.0
Manafaru	6.9922	72.9414	1.2	0.0	1.0	1.0	0.1	0.0
Mashura Beyru	5.5429	73.5053	1.9	1.5	0.9	0.0	0.0	0.0
Mathiveri Beyru	4.1915	72.7365	2.4	1.3	0.9	1.0	0.0	0.0
Mathiveri Falhu	4.2065	72.7501	0.9	1.3	1.6	0.3	0.4	0.0
Mathiveri Kandu	4.1796	72.7411	2.6	0.0	1.8	0.5	0.2	0.0
Medhufinolhu Faru	4.5104	73.3743	2.0	0.0	1.2	1.0	0.1	0.0
Meedhupparu Faru	5.4524	72.9804	1.0	1.0	1.1	1.0	0.2	0.0
Mendhoo Beyru	1.7843	73.3912	3.6	3.3	1.7	1.5	0.0	0.0
Moofushi Bojamhadi	3.8764	72.7064	5.8	1.8	2.0	0.5	0.0	0.0
Moofushi Denagili	3.8857	72.7080	4.4	2.1	1.5	1.9	0.0	0.0
Mudakan	-0.6109	73.1538	9.1	0.0	8.7	1.0	0.1	0.0
Mulidhoo Aquarium	6.8421	73.0112	1.3	0.7	0.6	0.3	0.0	0.0
Muthaafushi Faru	5.0764	72.8833	1.2	0.0	1.1	1.0	0.3	0.0
Naainfaru Faru	6.2111	73.0039	1.1	4.0	1.1	2.0	0.2	0.0
Nalaguraidhoo Beyru	3.4723	72.7988	1.4	1.5	1.1	0.0	0.0	0.0

Olhuveli Corner	1.8067	73.4228	5.0	2.0	12.3	0.0	0.0	0.0
Olhuveli Falhu	3.8392	73.4425	1.6	0.0	1.6	2.8	0.1	0.1
Orimasvaru Faru	5.8586	73.2030	1.1	1.0	1.1	0.0	0.3	0.0
Orivaru Giri	5.7998	73.3097	1.1	0.0	1.2	1.0	0.2	0.5
Randheli Falhu	5.7041	73.3376	1.1	0.0	0.9	1.5	0.1	1.5
Rangabeelu Faru	4.4295	72.9563	1.5	0.0	1.0	1.0	0.0	0.0
Rangali Beyru	3.6135	72.7076	2.4	1.0	0.8	0.0	0.0	0.0
Rangali Falhu	3.6128	72.7245	1.7	1.0	2.6	1.5	0.2	0.0
Rangali Madivaru	3.5863	72.7183	1.8	3.2	0.6	0.3	0.0	0.0
Rasdho Madivaru	4.2635	72.9997	6.0	1.0	3.9	1.0	0.1	0.0
Rasfari North	4.4421	73.3617	2.0	2.8	0.7	0.1	0.0	0.0
Reethi Faru	5.5445	73.4859	1.2	1.0	1.1	0.5	0.1	0.0
Rihiveli Falhu	3.8143	73.3997	1.5	0.0	1.9	2.0	0.1	0.0
Sola Corner	5.4914	72.8331	2.4	4.5	1.4	1.8	0.1	0.0
Thundufushi Falhu	3.7853	72.7250	1.0	0.7	1.7	0.3	0.2	0.0
Thundufushi Thila	3.7906	72.7312	1.5	1.5	1.1	0.5	0.2	0.0
Vagaaru Beyru	7.0973	72.8733	2.1	1.2	0.6	1.2	0.0	0.2
Vakkaru Faru	5.1298	72.9112	1.1	0.0	1.6	1.0	0.3	1.0
Vavvaru Kandu	5.4251	73.3536	4.0	1.0	3.8	2.3	0.2	0.0
Veligadu Falhu	5.5320	73.4448	1.9	2.9	1.5	0.6	0.1	0.0
Veligandu Kandu	4.3227	73.0064	2.5	1.6	1.8	1.0	0.1	0.0
Vihamaafaru Falhu	4.1344	72.7459	4.9	1.0	2.3	0.6	0.0	0.0
Viligili Kandu Addu	-0.6721	73.2084	0.6	1.0	0.0	0.0	0.0	0.0
Vinaneiy Finolhu	5.3112	73.0904	1.3	0.7	1.3	1.3	0.2	0.3
Voavah Faru	5.3157	73.0800	1.8	2.0	1.4	4.0	0.0	1.0

Appendix II: Model Selection

Table S3. Explanatory co-variables used in generalised additive models (GAMs) for the response variable daily number of sightings of feeding adult manta rays. AIC was used for model selection and percent deviance explained (%DE) was used as an additional check of model fit. Model 1 is the saturated model and the selected model.

Model	Explanatory Co-Variates	%DE	AIC	Δ AIC
1	S(Depth) + S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	39.8	22339.74	0
2	S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	39.5	22362.72	22.98
3	S(Depth) + S(chl) + S(sst) + reef.type + season*atoll.side	38.3	22474.32	134.58
4	S(Depth) + S(Slope) + S(sst) + reef.type + season*atoll.side	39.3	22383.15	43.41
5	S(Depth) + S(Slope) + S(chl) + reef.type + season*atoll.side	39.3	22382.07	42.33

Table S4. Explanatory co-variables used in generalised additive models (GAMs) for the response variable daily number of sightings of feeding juvenile manta rays. AIC was used for model selection and percent deviance explained (%DE) was used as an additional check of model fit. Model 1 is the saturated model and the selected model.

Model	Explanatory Co-Variates	%DE	AIC	Δ AIC
1	S(Depth) + S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	23.3	20776.78	0
2	S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	22.6	20815.98	39.2
3	S(Depth) + S(chl) + S(sst) + reef.type + season*atoll.side	20.5	20947.96	171.18
4	S(Depth) + S(Slope) + S(chl) + reef.type + season*atoll.side	23.2	20779.94	3.16
5	S(Depth) + S(Slope) + S(sst) + reef.type + season*atoll.side	23.2	20778.05	1.27
6	S(Depth) + S(Slope) + reef.type + atoll.side*julian.day	23	20785.05	8.27

Table S5. Explanatory co-variables used in generalised additive models (GAMs) for the response variable daily number of sightings of feeding young of year (YoY) manta rays. AIC was used for model selection and percent deviance explained (%DE) was used as an additional check of model fit. Model 1 is the saturated model and model 3 was the selected model.

Model	Explanatory Co-Variates	%DE	AIC	Δ AIC
1	S(Depth) + S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	20.1	2680.375	1.779
2	S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	18.9	2701.952	23.356
3	S(Depth) + S(chl) + S(sst) + reef.type + season*atoll.side	20.1	2678.596	0
4	S(Depth) + S(Slope) + S(chl) + reef.type + season*atoll.side	18.7	2705.298	26.702
5	S(Depth) + S(Slope) + S(sst) + reef.type + season*atoll.side	19	2696.904	18.308

Table S6. Explanatory co-variables used in generalised additive models (GAMs) for the response variable probability a sighting is of a juvenile individual. AIC was used for model selection and percent deviance explained (%DE) was used as an additional check of model fit. Model 1 is the saturated model and the selected model.

Model	Explanatory Co-Variates	%DE	AIC	Δ AIC
1	S(Depth) + S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	21.9	15108.98	0
2	S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	21.8	15111.03	2.05
3	S(Depth) + S(chl) + S(sst) + reef.type + season*atoll.side	21.8	15112.16	3.18
4	S(Depth) + S(Slope) + S(sst) + reef.type + season*atoll.side	21.4	15157.33	48.35
5	S(Depth) + S(Slope) + S(chl) + reef.type + season*atoll.side	21	15202.67	93.69
6	S(chl) + S(sst) + reef.type + season*atoll.side	21.8	15110.91	1.93

The GAM model used to assess the probability of a sighting being a juvenile individual assumed a binomial distribution and considered sightings of juveniles (Juv.Sight) as successes and sightings of adults (Adult.Sight) as failures. The following R code was used to create the saturated model:

```
#create a binomial GAM where juvenile will be success, adult will be failure

#code this with cbind(successes, failures)

juv_success<-gam(cbind(Juv.Sight, Adult.Sight) ~ s(Depth, k=5) +
  s(Slope, k=5) + s(chl, k=5) + s(sst, k=5) + hab.type +
  season*atoll.side, family=binomial(link="logit"), data=df_feed)

#check model summary
summary(juv_success)

#view model smooth plots
plot.gam(juv_success, shade=TRUE, pages=1)

#check model diagnostic plots
gam.check(juv_success)
```

Table S7. Explanatory co-variates used in generalised additive models (GAMs) for the response variable daily number of sightings of cleaning adult manta rays. AIC was used for model selection and percent deviance explained (%DE) was used as an additional check of model fit. Poor model fit meant that these models were not analysed further.

Model	Environmental Co-Variates	%DE	AIC	Δ AIC
1	S(Depth) + S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	14.3	26377.54	0
2	S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	14.2	26378.47	0.93
3	S(Depth) + S(chl) + S(sst) + reef.type + season*atoll.side	12.8	26456.86	79.32
4	S(Depth) + S(Slope) + S(sst) + reef.type + season*atoll.side	14	26395.24	17.7
5	S(Depth) + S(Slope) + S(chl) + reef.type + season*atoll.side	13.6	26414.41	36.87
6	S(Slope) + S(chl) + reef.type + season*atoll.side	13.5	26413.64	36.1

Table S8. Explanatory co-variates used in generalised additive models (GAMs) for the response variable daily number of sightings of cleaning juvenile manta rays. AIC was used for model selection and percent deviance explained (%DE) was used as an additional check of model fit. Poor model fit meant that these models were not analysed further.

Model	Environmental Co-Variates	%DE	AIC	Δ AIC
1	S(Depth) + S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	4.09	15892.41	0
2	S(Slope) + S(chl) + S(sst) + reef.type + season*atoll.side	4.05	15892.9	0.49
3	S(Depth) + S(chl) + S(sst) + reef.type + season*atoll.side	3.55	15923.94	31.53
4	S(Depth) + S(Slope) + S(sst) + reef.type + season*atoll.side	4	15895.46	3.05
5	S(Depth) + S(Slope) + S(chl) + reef.type + season*atoll.side	3.74	15905.39	12.98
6	S(Slope) + S(chl) + reef.type + season*atoll.side	3.66	15907.56	15.15