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Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (*Mobula alfredi*) in the Maldives, implications for conservation

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Abstract

1. Reef manta rays (*Mobula alfredi*) are one of the ocean's largest and most charismatic species. Pressure from targeted and bycatch fisheries coupled with their conservative life-history traits including slow growth, late maturity, and low fecundity has led to catastrophic declines of the global population. The species is now listed as Vulnerable to Extinction on IUCN Red List of Threatened Species.
2. The global *M. alfredi* population is widely distributed in highly fragmented subpopulations. The Maldives supports the world's largest known subpopulation that undergoes seasonal migrations which are thought to be linked to peaks in ocean productivity induced by the South Asian Monsoon. Although the species is protected from targeted fisheries in the region, increasing pressures from habitat degradation and unsustainable tourism activities mean their effective conservation relies upon knowledge of the species' habitat use, seasonal distribution, and the environmental influences on such movements.
3. Photo-ID sighting records collected between 2005 and 2017 were used to identify key aggregation sites throughout the archipelago, and multiple linear regression and prediction analysis identified the environmental variables affecting variations in the intra-annual sighting frequency of *M. alfredi*.
4. *Mobula alfredi* were recorded at 273 different sites, 48 of which, with >100 sightings at each, were classified as key areas of habitat use. South-west monsoon winds and chlorophyll-*a* concentration predominantly affected the monthly percentage of *M. alfredi* sighted on the down-current side of the atolls.
5. In a country where climate change and touristic pressure are increasingly threatening this species and its habitat, the identification of key areas of habitat use and temporal changes in the use of these sites highlight the areas that should be prioritized for protection enabling more effective conservation management.

KEYWORDS
archipelago, climate change, conservation evaluation, endangered species, fishing, marine protected area, ocean, pollution

1 | INTRODUCTION

Reef manta rays (*Mobula alfredi*) are highly conspicuous, large zooplanktivorous elasmobranchs of the monogeneric Mobulidae family (mobulids), which currently includes nine species (Marshall, Compagno, & Bennett, 2009; White et al., 2017). *Mobula alfredi* are widely distributed throughout the tropical and sub-tropical waters of the Indo-West Pacific Ocean, although subpopulations appear to be highly fragmented (Couturier et al., 2012; Kashiwagi, Marshall, Bennett, & Ovenden, 2011), probably due to resource and habitat requirements (Stewart et al., 2018). *Mobula alfredi* frequent the coastal reefs of continents and remote oceanic islands (Kashiwagi et al., 2011), but also venture offshore and into the mesopelagic zone (Braun, Skomal, Thorrold, & Berumen, 2014; Jaine et al., 2014).

Target and bycatch fisheries (Croll et al., 2016), which are partly driven by a demand for mobulid gill plates for use in Asian medicine (O'Malley, Townsend, Hilton, Heinrichs, & Stewart, 2016), have resulted in *M. alfredi* population declines in recent decades (Lawson et al., 2017; Rohner et al., 2013; Ward-Paige, Davis, & Worm, 2013). Due to these declines, coupled with their conservative life history traits including slow growth, late maturity, and low fecundity (Lawson et al., 2017; Marshall & Bennett, 2010; Stevens, 2016; Stewart, Jaine, et al., 2018) they are now listed as Vulnerable to Extinction on the IUCN Red List of Threatened Species (Marshall et al., 2018).

Despite the economic value of *M. alfredi* to some local economies (Anderson, Adam, Kitchen-Wheeler, & Stevens, 2010; O'Malley, Lee-Brooks, & Medd, 2013), poorly managed tourism, development, and habitat degradation are increasingly impacting this species, especially at ecologically important aggregation sites (Murray et al., 2019; Rohner et al., 2013; Stevens & Froman, 2018; Venables, McGregor, Brain, & Van Keulen, 2016). Furthermore, the species is likely to be vulnerable to the impacts of climate change, such as rising sea surface temperatures, which have the potential to reduce the manta ray's food availability (Richardson, 2008). Therefore, to ensure the conservation of *M. alfredi*, there is a need to identify and effectively protect areas of important habitat for this species throughout its range (Stewart, Jaine, et al., 2018).

Site fidelity and migratory behaviour in *M. alfredi* have been linked to areas of high primary productivity and prey density (Armstrong et al., 2016; Jaine et al., 2014) and may also vary by sex and age-class (Couturier et al., 2011; Stewart, Nuttall, Hickerson, & Johnston, 2018. The 26 coral atolls that form the Maldives archipelago support the world's largest known subpopulation of *M. alfredi* (Kitchen-Wheeler, Ari, & Edwards, 2011; Stevens, 2016). The migratory behaviour of this subpopulation is strongly influenced by the South Asian Monsoon (SAM) (Anderson, Adam, & Goes, 2011), which drives currents that enhance productivity on the leeward side of the atolls through deep-water upwellings (Doty & Oguri, 1956; Sasamal, 2006), bringing nutrient-rich water into the euphotic zone (Deik, Reuning, & Pfeiffer, 2017; Sasamal, 2006). *Mobula alfredi* follow these productivity hotspots, migrating across the archipelago with the biannual reversal of winds and the concomitant ocean surface currents, exploiting the richest zooplankton feeding grounds (Anderson et al., 2010; Kitchen-Wheeler et al., 2011).

During each monsoon, *M. alfredi* use a variety of shallow reef habitats within the seasonal hotspot, favouring productive channels and lagoons that concentrate their prey (Kitchen-Wheeler, 2010; Stevens, 2016; Stevens, Hawkins, & Roberts, 2018). They also use nearby cleaning stations (Kitchen-Wheeler, 2010; Stevens, 2016; Stevens et al., 2018) where cleaner wrasse support their physical health (O'Shea, Kingsford, & Seymour, 2010) and intraspecies social interactions occur (Rohner et al., 2013).

Although all ray species are protected from target fisheries in the Republic of Maldives (EPA, 2014), the total combined area protected by the government consists of 42 marine protected areas (MPAs) that cover just 116.3 km^2, which is only 0.5% of the area (21,596 km^2) that falls within the boundaries of the 26 geographical atolls' outer rims (Stevens & Froman, 2018). Only one MPA, Hanifaru Bay, has a management plan (in place since July 2011), with on-site enforcement of the regulations (Stevens & Froman, 2018).

More effective protection of the Maldives' *M. alfredi* subpopulation is needed in the face of increasing pressures from habitat destruction, climate change, incidental bycatch, and tourism (Stevens & Froman, 2018). Effective protection relies heavily on a more detailed understanding of how the subpopulation utilise their environment and identification of the environmental factors that influence distribution. This study aims to assist conservation planning by using in-water manta ray photo-ID records, combined with environmental data, to: (1) identify locations used by this species throughout the archipelago; (2) identify the primary function of these sites for *M. alfredi*; (3) determine which environmental drivers influence site use; and (4) determine annual patterns in *M. alfredi* presence at these sites.

2 | METHODS

2.1 | Data collection

The Maldives archipelago extends 870 km from 7° north to half a degree south of the equator in the Indian Ocean (Figure 1). During a 13-year study, from 2005 to the end of 2017, over 15,000 surveys were undertaken throughout the Maldives at known *M. alfredi* aggregation sites, and opportunistically at other locations, to photographically record the individuals present. Environmental data on the wind and primary productivity were obtained for the same period.

2.1.1 | Manta rays

Identification photographs (photo-ID) were taken of the ventral side of the manta rays at aggregation sites throughout the Maldives. The images captured the unique gill-plate spot pattern, which can be used to identify the individual throughout its lifetime (Kitchen-Wheeler, 2010). These images also allow the sex and physical condition of the

FIGURE 1 The 48 sites identified as key *M. alfredi* habitats (>100 sightings) during NE (left map) and SW (right map) monsoon for the study period 2005–2017. Cleaning stations (blue circles) and feeding areas (red circles). Site numbers correspond to Table 1 (cleaning stations) and Table 2 (feeding areas)
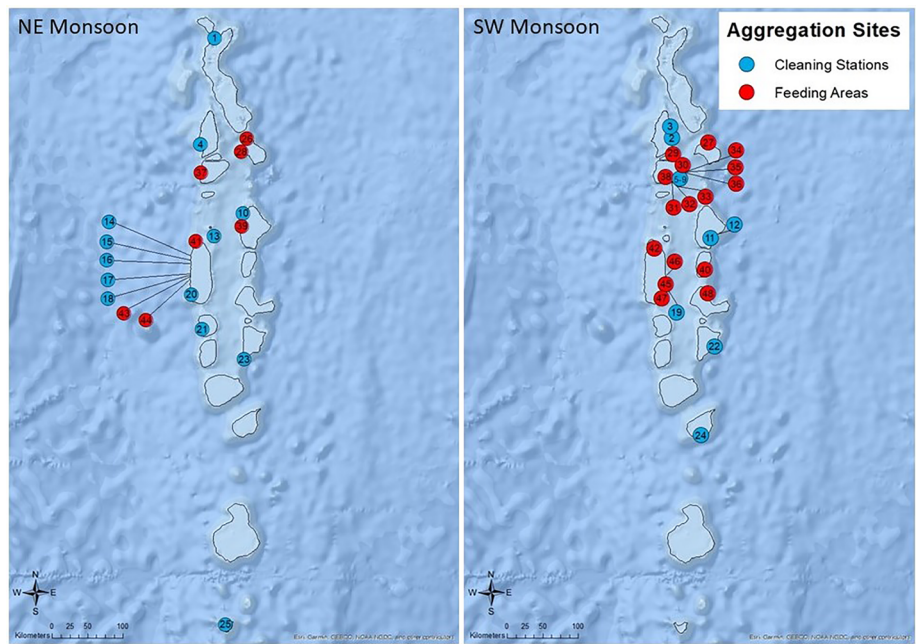
individual to be determined (Kitchen-Wheeler, 2010). In the context of this study, a *sighting* is defined as a confirmed photo-ID of an individual *M. alfredi* on a given day at a defined location. When manta rays were encountered, where possible, photo-ID and behavioural activity of each individual was recorded. Behavioural activity was broken down into four major groups: (1) feeding; (2) cleaning; (3) cruising; and (4) courtship. During an encounter, an individual may undertake several different activities. In these situations, the activity that dominated the encounter was recorded as the primary behaviour. A typical survey during this study was performed via scuba or freediving from either a dedicated research vessel or commercial diving vessels. Scuba surveys lasted on average 60 minutes and ranged to a maximum depth of 30 m. Freediving surveys lasted on average 120 minutes. Surveys were undertaken by one of the authors (Stevens, 2016), or by trained staff members or volunteers from the Manta Trust (www.mantatrust.org).

Surveys were performed at different times of day throughout the month in all months of the year. However, at the known *M. alfredi* aggregation sites, surveys were most likely to be undertaken during the period when sightings were most likely to occur, creating some sampling bias. Nonetheless, this dataset offers an opportunity to explore the distribution of this species throughout the Maldives in the most detailed way possible to date.

2.1.2 | Wind speed and direction

The Maldives south-west (SW) monsoon (season), or *Hulhangu*, occurs from May to October, while the north-east (NE) monsoon, or *Iruvai*, occurs from December to March each year, with the months of November and April considered as transitional periods of change in between (Anderson et al., 2010). However, the transition periods between the monsoons are highly variable, with reports that they also

extend into October and March (Aslam & Kench, 2017). Daily mean wind direction and wind speed data were obtained from the Maldives' Meteorological Service (MMS) in Malé. These data were used to calculate the monthly wind direction as the percentage of days in a month that the wind direction represented the NE monsoon (0–90°), or the SW monsoon (202.5–315°) (Anderson et al., 2011). Mean monthly wind percentage was calculated to show the annual period (season) of each monsoon and identify the months in which transition between the monsoons occurs. Monthly mean wind speed was calculated separately for days classified as having NE, SW or 'other' (i.e. neither NE nor SW) wind direction.

2.1.3 | Chlorophyll-a concentrations

Monthly 4-km^2 chlorophyll-a (Chl-*a*) data were obtained from NASA's Goddard Space Flight Centre's Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua (http://oceancolor.gsfc.nasa.gov). The data were extracted from each location where reef manta rays were sighted using the Marine Geospatial Ecology Tools package (Roberts, Best, Dunn, Treml, & Halpin, 2010) via ArcGIS. Monthly mean Chl-*a* concentration (mg/m^3) was then calculated separately for the east and the west side of the atolls using values for the days and locations where reef manta rays had been sighted that month.

2.2 | Data analysis

2.2.1 | Biannual migration

To assess biannual migration, the east and west side of the atolls were established by creating a map of the Maldives in ArcGIS 10.5 including polygons for each of the 26 geographical atolls. Two atolls

(Thiladhunmathi and Vaavu) have a 'lopsided' shape thus their polygons were subdivided giving a total of 30 polygons. Each atoll where sightings occurred was then divided into east and west by establishing the true centroid of each polygon using Calculate Geometry (Figure S1), the polygon was then divided into angle segments using Data Management Tools. All the sighting locations were then projected, and those within 1–179° were classified as east, and those within 181–359° were classified as west. All sightings were then integrated and projected as monthly total sightings at each location. Any locations with 1–4 sightings in the month were excluded to reduce the bias a small number of sightings may have on subsequent analysis. The effect on the total number of *M. alfredi* ($log^{10}(y+1)$) sightings on each side of the atoll (east, west) and monsoon (SW, NE) was assessed by two-way analysis of variance (ANOVA) (R 3.5.2; R Core Team, 2013).

2.2.2 | Environmental influences

The influence of environmental variables on the monthly percentage of *M. alfredi* sighted on the east and the west side of the atolls was explored with multiple linear regression (MLR) modelling (R 3.5.2; R Core Team, 2013). For example, in October 2013, there was a total of 1,142 *M. alfredi* sightings; of these 1,106 were observed on the east side of the atolls and 36 were observed on the west, giving 96.84% on the east side of the atolls and 3.16% on the west. The percentage of *M. alfredi* sighted on the east and west were modelled independently. To correct the non-normal distribution of the response variables, they were transformed to their difference from the mean, ignoring the sign of difference using the following form:

$$|(y - mean(y))|$$

For each side of the atoll, combinations of one to six explanatory variables were tested including: (1) monthly percentage of days the wind direction represented the NE and (2) SW monsoons; (3) mean monthly wind speed of NE and (4) SW monsoon winds; (5) mean monthly wind speed for the 'other' days (i.e. winds neither NE or SW monsoon); and (6) mean monthly Chl-*a* concentration on the west side of the atolls for the west models and east side for the east models. For example, when investigating the environmental influences of the changes in the monthly percentage of manta rays sighted on the east side of the atolls (EMAN), a model was constructed to include combinations of one to all six of the aforementioned variables, e.g. EMAN ~ the mean monthly wind speed of the SW monsoon winds (SWWS) + the mean Chl-*a* concentration on the east side of the atolls (ECHLA) and EMAN ~ SWWS + ECHLA + monthly SW monsoon wind frequency (the percentage of days each month that the wind direction represented the SW monsoon [202.5–315°], WDSW).

The order of incorporation of the explanatory variables into the model was determined by Regsubsets of the 'leaps' R package (Lumley, 2017). An assessment of autocorrelation was made by visual inspection of the autocorrelation function (ACF) plot of residuals,

followed by a Durbin–Watson test from the 'lmtest' library (Millo & Mitchell, 2017). Models that did not meet the requirements of the Durbin–Watson test (Field, Miles, & Field, 2012) were excluded from analysis. Models were then validated through an inspection of residuals and the application of Global Validation of Linear Models Assumptions of the 'gvlma' R package (Pena & Slate, 2006). Models that did not satisfy all assumptions were also excluded from the analysis.

An information theoretic approach was adopted to provide a quantitative measure of relative support via ranking and weighting of models thus allowing some inferences to be made about all models (Burnham & Anderson, 2002). Rank was established using corrected Akaike information criterion (AIC_c) test statistic, which is an asymptotically unbiased estimator of model quality (Burnham & Anderson, 2002). Models are not assessed by the absolute size of AIC_c but by their relative values over candidate models, particularly the differences between AIC_c values ($_\Delta AIC_c$) (Burnham & Anderson, 2002). $_\Delta AIC_c$ is calculated using the following form where i is the model:

$$\Delta_i = AICc_i - AICc_{min},$$

The relative merits of the models were assessed based on the criteria specified by Burnham and Anderson (2002) where the model estimated to have the greatest support has

$$\Delta_i \equiv \Delta_{min} \equiv 0$$

while models with $_\Delta AIC_c < 2$ are considered to have substantial support, models with 4–7 $_\Delta AIC_c$ have considerably less support, and those with $_\Delta AIC_c > 10$ have essentially no support (Burnham & Anderson, 2002). Plausible models for the current study were identified as those with $_\Delta AIC_c < 2$ and all other models were excluded from the analysis except the null model which was retained for comparison.

To effectively scale and interpret the Δ_i values of the chosen models, Akaike weights ($_w AIC_c$) were calculated using the following form where R is the set of models:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_r\right)}$$

Therefore, $_w AIC_c$ is relative to the set of chosen models and ranges from 0 (no support) to 1 (complete support). AIC_c, $_\Delta AIC_c$, and $_w AIC_c$ were obtained using the 'MuMin' R package (Bartoń, 2018).

The accuracy of an estimated parameter was inferred from 95% confidence intervals (CIs) for the slope (β). A narrower CI range implies a more precise estimation while a CI that does not span zero indicates that the null hypothesis may be rejected (Arnold, 2010). For the current study, CI was calculated using the 'MASS' R package (Brian, Venables, Bates, Firth, & Ripley, 2018).

To remediate uninformative parameters, model averaging using the full-model averaging approach was conducted using the 'MuMin'

R package (Bartoń, 2018) whereby the β is averaged across the set of competing models (Burnham & Anderson, 2002).

Model averaging calculates a weighted average of parameter estimates, $\hat{\beta}_i$ across all models, those including and excluding $\hat{\beta}_i$. The estimator is

$$\tilde{\bar{\beta}} = \sum_{j=1}^{R} w_j \hat{\beta}_{ij}$$

where $\hat{\beta}_{ij} \equiv 0$ if variable i is not included in model j (Burnham & Anderson, 2002).

2.2.3 | Predictive models

The environmental variables of the most plausible model(s) identified through MLR were used to predict monthly *M. alfredi* percentages on the east, and the west side of the atolls for each month where all environmental variable data were available between 2005 and 2017 utilizing the predict() function of the 'MuMin' R package (Bartoń, 2018).

The prediction parameters were set using the environmental variables from each month, and the accuracy of predictions was assessed by comparing the results to the actual percentage of manta rays observed.

Error margins for the difference between the predicted and actual monthly percentages of *M. alfredi* on the east and west side of the atolls were deemed accurate if <15%, acceptable if 15–20%, and inaccurate if >20%.

The overall difference between predicted and actual percentages of *M. alfredi* on the east and the west side of the atolls was tested with a Wilcoxon signed-rank test in R.

3 | RESULTS

3.1 | Manta ray sightings and site type

A total of 54,605 photo-ID sightings of 4,411 individual *M. alfredi* were recorded from 21 atolls at 273 different sites. Three types of site were identified: 67 (25%) were considered primarily as cleaning stations because *M. alfredi* were predominantly engaged in cleaning

TABLE 1 Reef manta ray cleaning station aggregation sites with >100 sightings in 2005–2017 (*n* = 25) throughout the 26 atolls of the Maldives archipelago. Latitude and longitude are given in decimal degrees; Monsoon is either north-east (NE) or south-west (SW)

Site	Atoll	Site name	Latitude	Longitude	Reef	Monsoon	Sightings	Individuals
1	Thiladhunmathi	Mulidhoo Aquarium	6.842	73.011	Outer	NE	147	120
2	Raa	Kottefaru Beyru	5.514	73.048	Outer	SW	209	156
3	Raa	Neyo Beyru	5.492	73.043	Outer	SW	259	183
4	Raa	Sola Corner	5.491	72.833	Outer	NE	259	177
5	Baa	Dhonfanu Faru	5.183	73.124	Inner	SW	123	113
6	Baa	Dhigu Thila	5.174	73.108	Inner	SW	627	441
7	Baa	Dharavandhoo Thila	5.161	73.123	Inner	SW	108	99
8	Baa	Dharavandhoo Corner	5.156	73.142	Outer	SW	1,672	521
9	Baa	Nelivaru Thila	5.126	73.079	Inner	SW	119	105
10	North Malé	Rasfari North	4.442	73.362	Outer	NE	1,197	266
11	North Malé	Sunlight Faru	4.300	73.534	Inner	SW	594	206
12	North Malé	Lankan Beyru	4.280	73.557	Outer	SW	4,642	511
13	Rasdhu	Veligandu Kandu	4.323	73.006	Channel	NE	225	105
14	Ari	Dhonkalo Thila	3.971	72.717	Channel	NE	340	201
15	Ari	Himendhoo Rock	3.948	72.713	Outer	NE	213	131
16	Ari	Moofushi Denagili	3.886	72.708	Outer	NE	101	75
17	Ari	Moofushi Bojamhadi	3.876	72.706	Outer	NE	1,232	281
18	Ari	Kalhahandhi Huraa	3.798	72.705	Outer	NE	128	90
19	Ari	Okalhu Thila	3.681	72.959	Inner	SW	101	70
20	Ari	Rangali Madivaru	3.586	72.718	Outer	NE	841	192
21	Faafu	Kuda Falhu	3.141	72.859	Outer	NE	111	48
22	Meemu	Muli Kandu	2.926	73.589	Channel	SW	133	57
23	Meemu	Kurali Kandu	2.758	73.387	Outer	NE	233	50
24	Laamu	Hithadhoo Corner	1.798	73.410	Outer	SW	2,611	112
25	Addu	Mudakan	−0.611	73.154	Channel	NE	607	70

activities, 104 (38%) as feeding areas, while at the remaining
102 (37%) sightings consisted mostly of animals travelling through the
area (cruising). Most of the cleaning stations (81%, n = 54) were situ-
ated on shallow coral reef (≤20 m) of atoll kandus (channels), predomi-
nantly at the southern outer reef corner of the channel. Twenty-five
of the cleaning stations had >100 sightings of at least 48 different
M. alfredi at each across the study period (Table 1 and Figure 1). The
cleaning station with the highest number of records was Lankan Beyru
in North Malé Atoll (Figure 1, site 12), with 4,642 sightings of 511 dif-
ferent M. alfredi.

Most of the feeding areas (87%, n = 90) were situated in the atoll
kandus, or inside the protected atoll falhus (lagoons) and farus (reefs).
Twenty-three of the feeding areas had >100 sightings of at least
73 different M. alfredi across the study period (Table 2 and Figure. 1).
The feeding area with the highest number of sightings was Hanifaru
Bay (Site 36) in Baa Atoll, with 20,892 sightings of 1,663 different
M. alfredi.

Overall, 4,014 individual M. alfredi were sighted at the 48 key
aggregation sites; 3,124 were sighted more than once, of which 2,588
were only sighted within the same atoll, and 755 were always seen at
the same site. Of the 2,369 individuals sighted at more than one site,
1,352 were predominantly sighted at one location (>55% of sightings
were at the same site).

3.2 | Wind direction

Mean monthly wind direction percentage indicated that that the SW
monsoon occurred from April until November, and the NE monsoon
runs from December to March. The transition months appeared to be
November/December between the SW and NE monsoon, and
March/April between the NE and SW monsoon (Figure 2).

3.3 | Biannual migration

More sightings of M. alfredi were on the east side of atolls during the
SW monsoon and more on the west side during the NE monsoon
(Figure S2). The significant interaction between the side of atolls and
the monsoon period ($F_{1, 44}$ = 55.59, P < 0.001) supports this conclu-
sion. These results support the biannual east–west and west–east
migration pattern reported by Anderson et al. (2011).

3.4 | Environmental influences

The influence of the environmental factors measured (Table 3) on the
monthly percentage of manta rays on the west side of the atolls

TABLE 2 Reef manta ray feeding area aggregation sites with >100 sightings in 2005–2017 (n = 23) throughout the 26 atolls of the Maldives archipelago. Latitude and longitude are given in decimal degrees; Monsoon is either north-east (NE) or south-west (SW)

Site	Atoll	Site name	Latitude	Longitude	Reef	Monsoon	Sightings	Individuals
26	Lhaviyani	Huravalhi Finolhu	5.525	73.439	Inner	NE	281	102
27	Lhaviyani	Fushifaru Kandu	5.490	73.522	Channel	SW	340	144
28	Lhaviyani	Dhanifaru	5.398	73.356	Inner	NE	499	182
29	Fasdhūetherē	Bathalaa Kandu	5.362	73.060	Channel	SW	738	187
30	Baa	Reethi Falhu	5.252	73.177	Lagoonal	SW	1887	590
31	Baa	Veyofushi Falhu	5.246	73.149	Lagoonal	SW	2,291	487
32	Baa	Dhandhoo Falhu	5.225	73.179	Inner	SW	215	151
33	Baa	Andhagiri	5.222	73.164	Inner	SW	313	226
34	Baa	Hurai Faru	5.207	73.162	Channel	SW	1,239	436
35	Baa	Hanifaru Beyru	5.175	73.161	Outer	SW	1,379	558
36	Baa	Hanifaru Bay	5.173	73.146	Channel	SW	20,892	1,663
37	Baa	Maa Faru Falhu	5.132	72.841	Lagoonal	NE	120	78
38	Baa	Maaneigaa	5.074	72.968	Lagoonal	SW	322	175
39	North Malé	Boduhithi Thila	4.451	73.362	Channel	NE	108	89
40	South Malé	Guraidhoo Falhu	3.898	73.461	Inner	SW	174	73
41	Ari	Gangehi Falhu	4.260	72.778	Lagoonal	NE	203	126
42	Ari	Genburugau Falhu	4.170	72.827	Lagoonal	SW	148	81
43	Ari	Maavaru Falhu	3.854	72.728	Lagoonal	NE	803	215
44	Ari	Maavaru Beyru	3.814	72.702	Outer	NE	152	107
45	Ari	Dhiggaru Kandu	3.715	72.971	Channel	SW	1,092	264
46	Ari	Huravalhi Falhu	3.688	72.963	Channel	SW	373	182
47	Ari	Dhigurah Falhu	3.536	72.918	Lagoonal	SW	951	207
48	Vaavu	Miyaru Kandu	3.598	73.499	Channel	SW	192	85

FIGURE 2 Mean monthly wind direction percentage (2005–2017) using the monsoon directions identified by Anderson et al. (2011) (NE = 0–90° SW = 202.5–315°). North-east monsoon wind percentage is transformed ($\chi^*- 1$) to show clearly the monthly variations
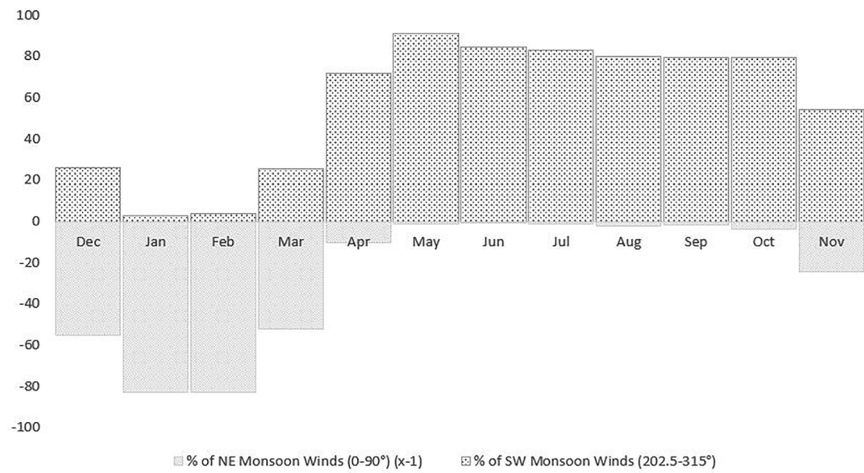
TABLE 3 Abbreviations and description of the variables used in models

Abbreviation	Variable	Variable description
EMAN	East manta rays	Monthly percentage of manta rays on the east of the atolls.
WMAN	West manta rays	Monthly percentage of manta rays on the west of the atolls.
WDSW	Wind direction south-west	The percentage of days each month that the wind direction represented the SW monsoon (202.5–315°)
SWWS	Southwest wind speed	Monthly mean SW monsoon wind speed.
WDNE	Wind direction north-east	The percentage of days each month that the wind direction represented the NE monsoon (0–90°)
NEWS	Northeast wind speed	Monthly mean NE monsoon wind speed.
OTSW	Other wind speed	Monthly mean wind speed of 'other' directions.
ECHLA	East Chl-a	Monthly mean chlorophyll-a concentration on the east side of the atolls.
WCHLA	West Chl-a	Monthly mean chlorophyll-a concentration on the west side of the atolls.

TABLE 4 Multiple linear regression results of plausible models ($_\Delta AIC_c < 2$) where the response variable is the monthly percentage of manta rays on the west side of the atolls (WMAN)

Model	Variables	df	AICc	ΔAICc	wAICc (ΔAICc <2)	R^2	P-value	F-value
W8	SWWS+WDSW	4	−142.1	0	0.635	0.22	<<0.001	$_{2, 106}$ 16.28
W15	SWWS+WCHLA	4	−141	1.11	0.365	0.22	<<0.001	$_{2, 106}$ 16.21
W0	NULL	2	−116.3	25.8	0	n/a	n/a	n/a

(WMAN) was assessed by MLR modelling. Two plausible models within the $_\Delta AIC_c < 2$ threshold were produced (Table 4). The highest-ranking model (W8) with the lowest AIC_c and the greatest relative weight ($_\Delta AIC_c = 0$, $_w AIC_c = 0.635$) suggested that increasing monthly mean SW monsoon wind speed (SWWS) and monthly SW monsoon wind percentage (WDSW) decreased WMAN (Figure 3). The second plausible model (W15) indicates increasing SWWS and decreasing monthly mean Chl-a concentration on the west side of the atolls (WCHLA) reduced WMAN (Figure 4).

Model W8 had the highest relative weight of the two models (W8: $_w AIC_c = 0.635$, W15: $_w AIC_c = 0.365$); however, both models appeared to explain the same amount of variation in WMAN (W8: $F_{2,106} = 16.28$, $R^2 = 0.22$, $P << 0.001$, W15: $F_{2,106} = 16.21$, $R^2 = 0.22$).

The 95% CI for the explanatory variables of each of the models and the averaged model (Figure 5) showed that the CI for SWWS was consistent throughout the models and had the narrowest range, which did not span zero, indicating that the null hypothesis for this variable may be rejected (Arnold, 2010). The wider CI of WDSW (−0.164, 0.046) in model W8 and WCHLA (−0.098, 0.144) in model W15, which both spanned zero, indicated that these variables were both less precise estimators for WMAN. Therefore, both W8 and W15 had relatively significant standing and may serve equally well in approximating WMAN.

The influence of the environmental factors measured (Table 3) on the monthly percentage of manta rays on the east side of the atolls (EMAN) was assessed by multiple linear regression modelling. Four
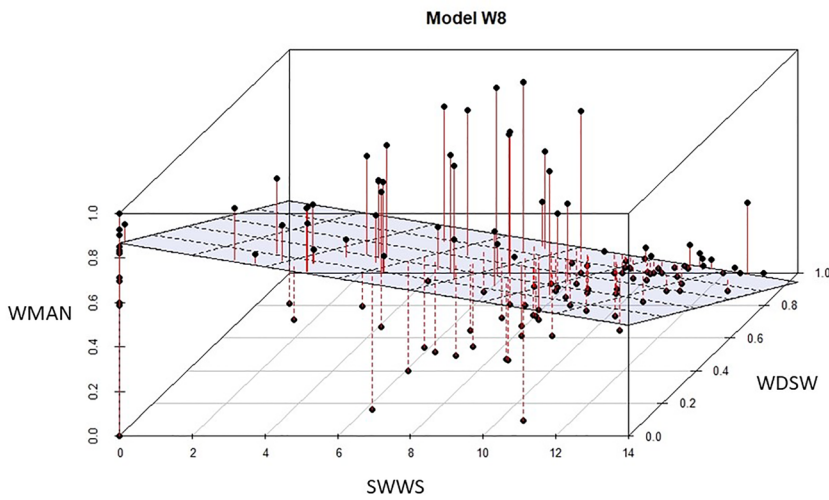
FIGURE 3 Relationship between the monthly percentage of manta rays on the west side of the atolls (WMAN) and the variables identified by model W8 (monthly mean SW monsoon wind speed, SWWS+ the percentage of days each month that the wind direction represented the SW monsoon (202.5–315°, WDSW) with regression plane of best fit to data points
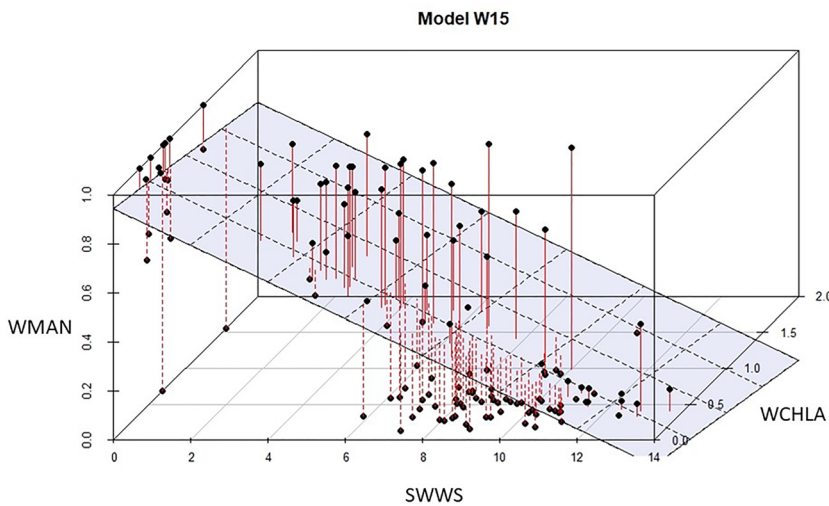
FIGURE 4 Relationship between the monthly percentage of manta rays on the west side of the atolls (WMAN) and the variables identified by model W15 (monthly mean SW monsoon wind speed, SWWS+ mean chlorophyll-a concentration on the west side of the atolls, WCHLA) with regression plane of best fit to data points

plausible models within the $_\Delta AIC_c$ < 2 thresholds were produced (Table 5). Model E15 is the highest-ranking model ($_\Delta AIC_c$ = 0, $_w AIC_c$ = 0.367) which indicated increasing SWWS and monthly mean Chl-*a* concentration on the east side of the atolls (ECHLA) increased EMAN (Figure 6).

The model explained 20% of the variation in EMAN ($F_{2,106}$ = 14.80, R^2 = 0.20, P << 0.001). All four models within the $_\Delta AIC_c$ < 2 thresholds contain SWWS and ECHLA and explained a similar amount of variation, but with the mean NE monsoon wind speed, monthly NE monsoon wind frequency, and WDSW as additional variables in models E25, E17, and E18, respectively, which indicated that these variables did not improve model E15. Multi-model inference via CI and model averaging (Figure 7), provided evidence that the variables of model E15 were useful parameters as neither spanned zero (Arnold, 2010), although the CI of ECHLA was relatively wide. In all other models, the additional variables spanned zero; thus, E15 may be considered the most plausible model.

3.5 | Prediction models

The models W8, W15, and E15 were used to predict the monthly percentage of manta rays on one side of atolls. These predictions were then compared with the actual monthly percentages observed; when assessing the accuracy of predictions, an absolute difference of <15% between predicted and observed percentage was deemed accurate and 15–20% acceptable. Prediction accuracy was assessed across three different time periods (months, years, monsoons). For model W8 (WMAN ~ SWWS + WDSW), 80 months of the 153 for which data were available were accurately predicted (|prediction-actual difference| < 15%), 16 months were acceptable (|prediction-actual difference|15–20%) and the remaining 57 months had differences >20% (Table S1). There was no significant difference between W8 predicted and observed WMAN (Wilcoxon matched-pairs signed ranks test, Z = 0.143, P > 0.05). Annual prediction differences (Figure 8) were accurate for four of the 13 years (2007, 2014, 2015, and 2016) and acceptable for four more years (2005, 2009, 2010, and 2017).

FIGURE 5 Point estimate of the monthly percentage of manta rays on the west side of the atolls (WMAN)| $(y - mean\ (y))$|with respective +/− 95% confidence interval of each variable in the west models within the $_\Delta AIC_c < 2$ threshold. SWWS = monthly mean SW monsoon wind speed, WDSW = the percentage of days each month that the wind direction represented the SW monsoon (202.5–315°), WCHLA = monthly mean chlorophyll-a concentration on the west side of the atolls
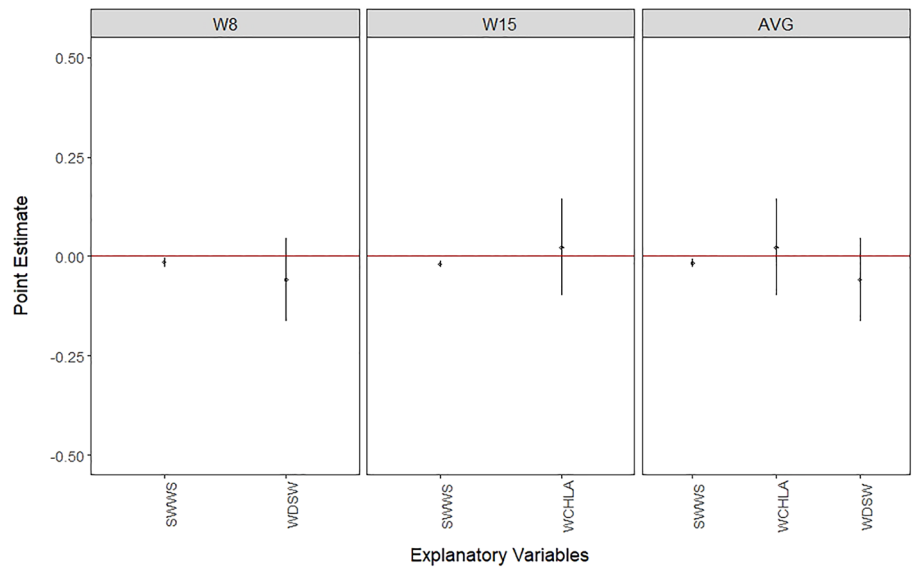
TABLE 5 Multiple linear regression results of plausible models ($_\Delta AIC_c < 2$) where the response variable is the monthly percentage of manta rays on the east side of the atolls (EMAN)

| Model	Variables	df	AICc	ΔAICc	wAICc (ΔAICc <2)	R^2	P-value	F-value
E15	SWWS+ECHLA	4	−143.6	0	0.367	0.20	<<0.001	$_{2,\ 106}$ 14.80
E25	SWWS+ECHLA+NEWS	5	−143	0.63	0.268	0.20	<<0.001	$_{3,\ 105}$ 10.39
E17	SWWS+ECHLA+WDNE	5	−142.3	1.28	0.194	0.20	<<0.001	$_{3,\ 105}$ 10.17
E18	SWWS+WDSW+ECHLA	5	−142.1	1.53	0.171	0.19	<<0.001	$_{3,105}$ 9.99
E0	NULL	2	−119.3	24.3	0	n/a	n/a	n/a
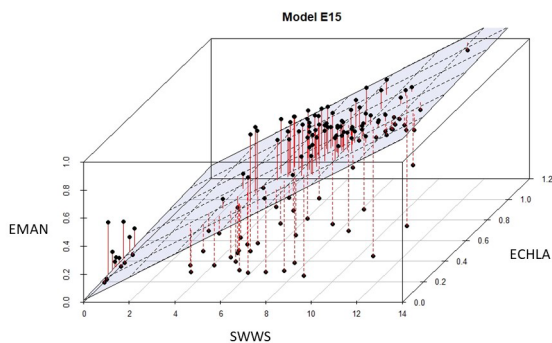
FIGURE 6 Relationship between the monthly percentage of manta rays on the east side of the atolls (EMAN) and the variables identified by model E15 (monthly mean SW monsoon wind speed, SWWS + mean chlorophyll-a concentration on the east side of the atolls, ECHLA) with regression plane of best fit to data points

Monsoon months were predicted accurately for nine of the 13 years; in the other years, predictions were acceptable. However, for the transition only months (March, April, November, and December), the differences were > 20% in all 13 years.

For model W15 (WMAN ~ SWWS + WCHLA), 57 of the 132 months for which data were available were accurately predicted,

13 months were acceptable and the remaining 62 months had differences >20% (Table S1). There was no significant difference between W15 predicted and observed WMAN (Wilcoxon matched-pairs signed ranks test, $Z = 0.06$, $P > 0.05$). Annual prediction differences (Figure 9) were accurate for one of the 13 years (2014) and acceptable for five more (2007, 2009, 2016, 2015, and 2014). The prediction difference for monsoon months was accurate for four (2007, 2014, 2015, and 2016) of the 13 years and acceptable for five more years (2005, 2008, 2009, 2013, and 2017). For the transition months (March, April, November, and December), predictions were acceptable for two years (2009 and 2011).

A single model (E15, EMAN ~ SWWS + ECHLA) best identified environmental variables influencing the percentage of manta rays on the east side of atolls. Of the 142 months for which data were available, the prediction differences of 64 months were accurate, and a further 11 months were acceptable. The remaining 67 months were >20% (Table S1). There was no significant difference between E15 predicted and observed EMAN (Wilcoxon matched-pairs signed ranks test, $Z = 0.398$, $P > 0.05$). Annual prediction differences (Figure 10) were accurate for one (2014) of the 13 years and acceptable for six more years (2007, 2009, 2011, 2013, 2015, and 2016). Predictions differences for the monsoon months were accurate for six years (2006, 2010, 2013, 2014, 2015, and 2016) and acceptable for five more years (2005, 2007, 2009, 2011 and 2017). For the
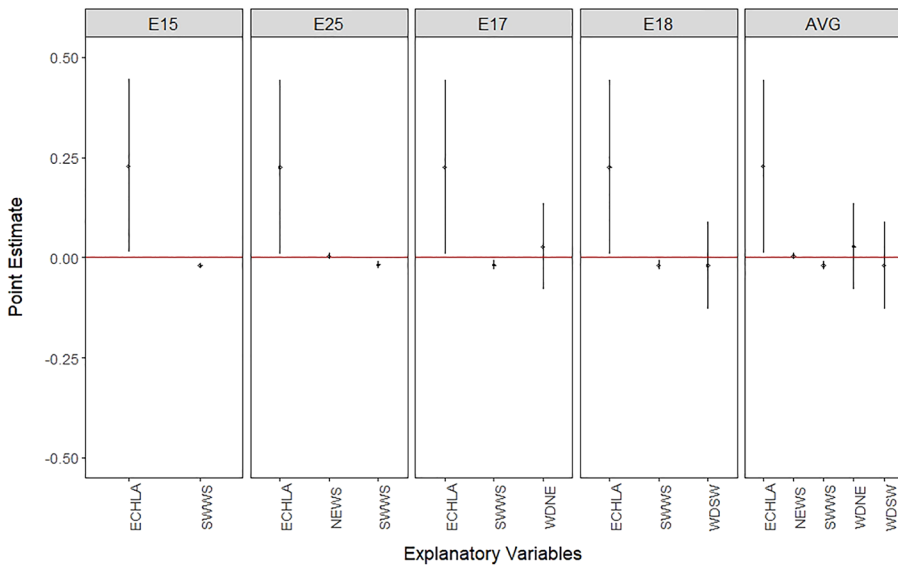
FIGURE 7 Point estimate of the monthly percentage of manta rays on the east side of the atolls (EMAN)|$(y - mean\ (y))$|with respective +/− 95% confidence interval of each variable in the east models within the $_\Delta AIC_c < 2$ threshold. SWWS = monthly mean SW monsoon wind speed, WDSW = the percentage of days each month that the wind direction represented the SW monsoon (202.5–315°), ECHLA = monthly mean chlorophyll-a concentration on the east side of the atolls, NEWS = monthly mean northeast monsoon wind speed, WDNE = the percentage of days each month that the wind direction represented the NE monsoon (0–90°)
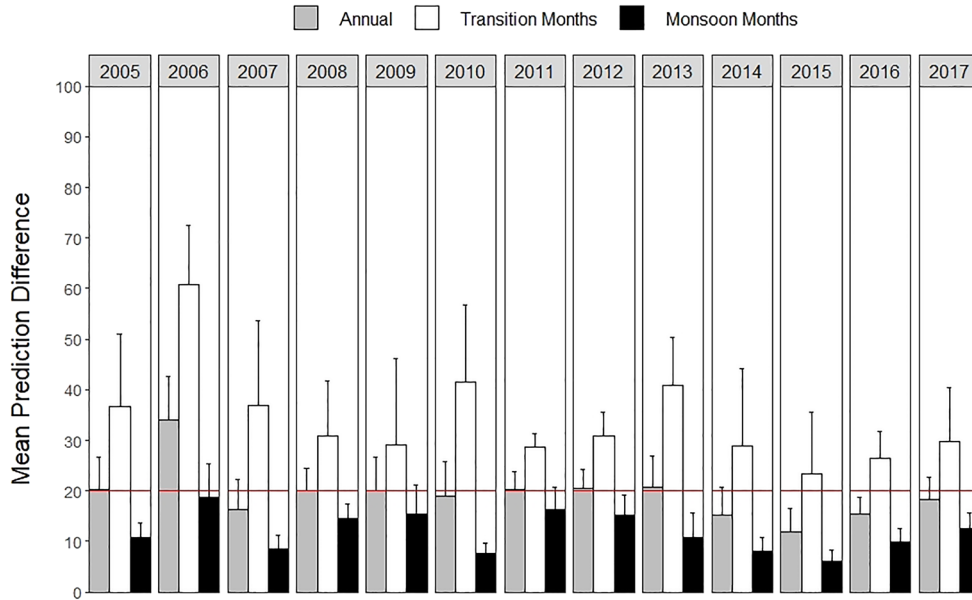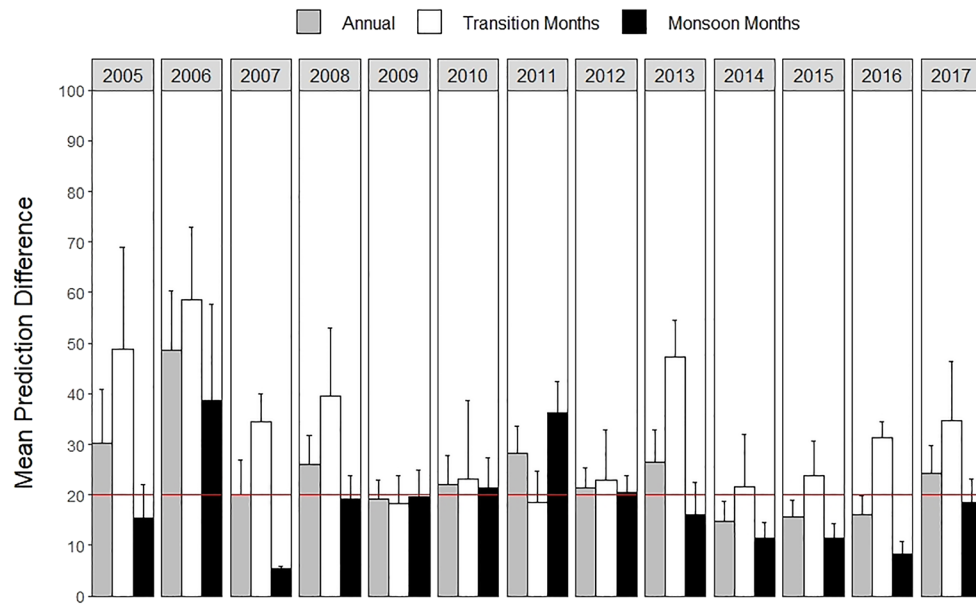

FIGURE 8 Mean prediction difference between the actual monthly percentage of manta rays on the west side of the atolls (WMAN) observed each year and the WMAN calculated by R predict() function using the variables identified by model W8 (monthly mean SW monsoon wind speed, SWWS + the percentage of days each month that the wind direction represented the SW monsoon (202.5–315°, WDSW). Shown as mean annual prediction difference, prediction difference for transition months only (March, April, November, and December) and prediction difference for monsoon months only (January, February, May–October), all with +SE. The red line shows the acceptable mean prediction difference threshold (20%)

transition months (March, April, November, and December), predictions were acceptable for three years (2009, 2011, and 2014).

4 | DISCUSSION

This study identified 171 *M. alfredi* aggregation sites throughout the Maldives archipelago; 48 of which were feeding areas or cleaning

stations that, based on the high number of individuals sighted, were considered areas of key habitat use. Cleaning stations provide essential benefits for *M. alfredi*, such as parasite removal, as well as social and reproductive interactions (Stevens, 2016; Stevens et al., 2018), while feeding hot-spots provide the concentrated food source required for their energetically efficient foraging strategies (Armstrong et al., 2016; Stevens, 2016). It is likely that more key aggregation sites exist, especially in regions of the country (the

FIGURE 9 Mean prediction difference between the actual monthly percentage of manta rays on the west side of the atolls (WMAN) observed each year and the WMAN calculated by R predict() function using the variables identified by model W15 (monthly mean SW monsoon wind speed, SWWS + mean chlorophyll-a concentration on the west side of the atolls, WCHLA). Shown as mean annual prediction difference, prediction difference for transition months only (March, April, November, and December) and prediction difference for monsoon months only (January, February, May–October), all with +SE. The red line shows the acceptable mean prediction difference threshold (20%)
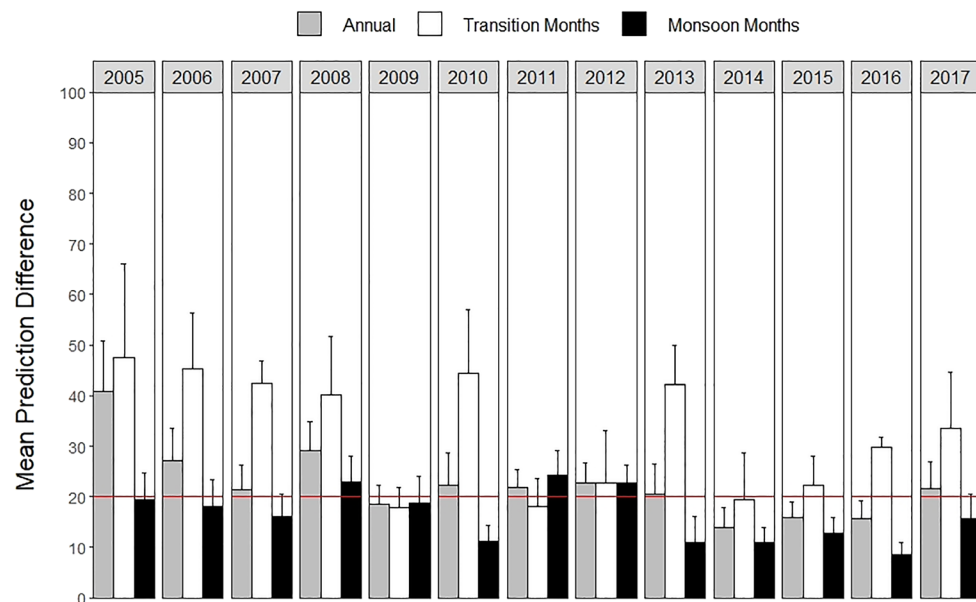
FIGURE 10 Mean prediction difference between the actual monthly percentage of manta rays on the east side of the atolls (EMAN) observed each year and the EMAN calculated by R predict() function using the variables identified by model E15 (monthly mean SW monsoon wind speed, SWWS + mean chlorophyll-a concentration on the east side of the atolls, ECHLA). Shown as mean annual prediction difference, prediction difference for transition months only (March, April, November, and December) and prediction difference for monsoon months only (January, February, May–October), all with +SE. The red line shows the acceptable mean prediction difference threshold (20%)

northernmost atolls) where surveys were less frequently undertaken. However, the extensive nature of this study, both spatially and temporally, means that many of the key aggregation sites, within the shallow (<30 m) reef systems of the Maldives, will have been recorded.

The current study also provides quantitative evidence that *M. alfredi* migrates east–west and west–east biannually, supporting previous observations (Anderson et al., 2011; Kitchen-Wheeler et al., 2011). The results of MLR modelling and prediction analysis

suggests that this distribution pattern was predominantly influenced by the SW monsoon winds and Chl-*a* concentration. The model for the east side of the atolls (E15; mean SW monsoon wind speed, SWWS + mean Chl-*a* on the east side of the atolls, ECHLA), linked the increase in the percentage of manta rays on the east side of the atolls (EMAN) to productivity enhanced by the strong ocean surface currents induced by the SW monsoon winds (Deik et al., 2017; Sasamal, 2006). On the west side of the atolls, productivity is increased by the NE monsoon winds (Sasamal, 2006); however, these winds are dominated by the onset and retreat of prevalent SW monsoon (Schott & McCreary, 2001). Both of the plausible models for the west side (W8; SWWS + SW monsoon wind frequency, WDSW. W15; SWWS + monthly mean Chl-*a* concentration on the west side of the atolls, WCHLA) identified the effect of SW monsoon winds – decreased wind speed increased primary production on the west side, increasing the percentage of manta rays observed (WMAN).

The model results highlight the prominent role of the SW monsoon in driving productivity, which supports the Maldives *M. alfredi* subpopulation. In particular, the longer duration of the SW monsoon means a comparatively longer period of enhanced primary production (Strutton et al., 2015). Moreover, as primary productivity can be suppressed during the NE monsoon due to the inflow of low-salinity surface waters from the eastern Indian Ocean and Bay of Bengal (Bruce, Johnson, & Kindle, 1994; Schulte, Rostek, Bard, Rullkötter, & Marchal, 1999), there might be greater food availability during the SW monsoon. Reef manta fecundity is linked to food availability (Ramirez-Llodra, 2002; Stevens, 2016), and productivity peaks that occur towards the end of the SW monsoon (Schulte et al., 1999) coincide with reproduction (Stevens, 2016).

Climate change has historically influenced primary production in the Indian Ocean through the intensification of the SAM winds (Gupta, Singh, Joseph, & Thomas, 2004). The modern SAM is influenced by anthropogenic climate change (Roxy et al., 2015). For example, emissions over India have subdued warming over land masses, reducing the land-sea thermal gradient (Roxy et al., 2015; Turner & Annamalai, 2012). The reduced thermal contrast affects the seasonal migration of the inter-tropical convergence zone, the shift of which is an essential component in the onset and retreat of the SW monsoon (Yadav, 2013). The strength of the SW monsoon is influenced by meteorological teleconnections, including two synoptic-scale jets, the low-level jet and tropical easterly jet (Kalapureddy, Rao, Jain, & Ohno, 2007). The low-level jet has been following a weakening trend since the 1950s; 'weak' spells in the SW monsoon with reduced wind speeds have increased by 30% (Joseph & Simon, 2005). A similar trend has been observed for the tropical easterly jet, which has been attributed to the cooling of land masses and warming of the Indian Ocean (Abish, Joseph, & Johannessen, 2013). The weakening of the SW monsoon winds intensifies ocean stratification and inhibits upwelling, thus lowering primary production in the Indian Ocean (Singh, Jung, Anand, Kroon, & Ganeshram, 2018). Enhanced stratification in the region is also driven by rising sea surface temperature, which is suggested to have decreased marine phytoplankton by up to 20% in the last 60 years (Roxy et al., 2016).

The predictable utilization of key aggregation sites and the large number of *M. alfredi* present suggest increased vulnerability to anthropogenic activities at these locations. Having identified the primary function of these key sites for *M. alfredi*, future conservation measures can now be focused more effectively. For example, the establishment of no-take MPAs at feeding locations would reduce manta ray vulnerability to fishing gear entanglement (Stevens & Froman, 2018), which can result in disfigurement and disablement (Deakos, Baker, & Bejder, 2011). It would also protect them from boat strikes and propeller injuries, which are common (Stevens & Froman, 2018) and have been highlighted as a major concern for *M. alfredi* subpopulations (Germanov & Marshall, 2014; Graham et al., 2012; Stewart, Jaine, et al., 2018). These threats also extend to other charismatic species in the Maldives (Stevens & Froman, 2018), including whale sharks (*Rhincodon typus*), with reports that as many as 40% of whale sharks encountered in the South Ari Atoll MPA bear injuries and scars caused by ocean vessels or other anthropogenic activities (Collins, 2013). At cleaning stations, MPAs can reduce damage from anthropogenic activities, which may degrade the habitat such as the intentional destruction of coral reefs to allow boat access and contact damage caused by divers and snorkellers (Stevens & Froman, 2018). Habitat degradation reduces live coral cover and in turn reef fish abundance (Jones, McCormick, Srinivasan, & Eagle, 2004) and cleaner wrasse activities (Arnal, Kulbicki, Harmelin-Vivien, Galzin, & Morand, 2002; Triki, Wismer, Levorato, & Bshary, 2018), potentially influencing reef manta ray visitation patterns (Barr & Abelson, 2019). If disruption of the mutualistically symbiotic relationship between cleaner fish and *M. alfredi* occurs, it could compromise the manta ray's fitness (Côté, 2000). Furthermore, at both cleaning stations and feeding areas, MPAs would mitigate *M. alfredi* vulnerability to disturbance by tourists in the water. While tourism is an essential part of the Maldives' economy (Anderson et al., 2010; O'Malley et al., 2013), unregulated tourism is escalating all the aforementioned threats, which may have deleterious impacts on the species. Murray et al. (2019) observed a significant negative influence on *M. alfredi* behaviour of various human behaviours during encounters. For instance, *M. alfredi* would abandon feeding if visitors came too close or obstructed their path (Murray et al., 2019). Although a short-term response to human interaction, disturbance is cumulative, and thus can incrementally develop into significant impacts (Venables et al., 2016). Semeniuk, Bourgeon, Smith, and Rothley (2009) found evidence of this in southern stingrays (*Dasyatus americana*) exposed to anthropogenic stressors arising from large crowds of tourist. In the Maldives, Anderson et al. (2010) reported *M. alfredi* aggregation sites with >100 divers and snorkellers present in 2008. A decade later, tourism visitor numbers to the Maldives have more than doubled (Stevens & Froman, 2018) significantly increasing the tourism pressures at these sites. As touristic pressures increase, they have the potential to drive manta rays away from important aggregation areas, reducing the fitness of individuals. For example, short-term disturbance, (e.g. Murray et al., 2019) and its cumulative effect, may cause manta rays to move away from key feeding habitats (Venables et al., 2016). Reduced food intake is likely to have

detrimental impacts including reduced fecundity and offspring survivorship (Stevens, 2016). Similarly, displacement from cleaning stations may impact breeding success, as these sites are important aggregation sites for reproductive activity (Stevens et al., 2018).

For an MPA to be effective, the designation of protection must also be accompanied by a comprehensive management plan which includes a code of conduct (CoC) and active enforcement (Venables et al., 2016). In the Maldives, a CoC and 10-step guide to sustainable tourism was published in 2017 (Murray et al., 2019) to help mitigate the impacts of touristic pressure (https://swimwithmantas.org/). However, due to the lack of government enforcement, compliance with these regulations is mainly voluntary (Murray et al., 2019). Without active enforcement, CoC compliance has been shown to be limited (Allen, Smith, Waples, & Harcourt, 2004; Murray et al., 2019) and the rate of compliance diminishes the longer the regulations remained unenforced (Schleimer et al., 2015).

The mitigation of touristic pressure via enforcement has been successful in the whale shark interaction industry operating within the Ningaloo Marine Park (an MPA in Western Australia), managed by the Western Australian Government Department of Parks and Wildlife (DPaW) (Venables et al., 2016). The MPA management plan uses precautionary management strategies (DPaW, 2013), which stem from the precautionary principle concept, that aim to protect people and the environment against uncertain risks of anthropogenic activities using anticipatory measures (UNESCO, 2005). The plan includes a CoC and other regulations that aim to minimize disturbance (DPaW, 2013). The other regulations include the requirement of an appropriate licence for operators, which comes with strict conditions that mitigate potential interference or harm to whale sharks (DPaW, 2013). The Ningaloo Marine Park MPA management plan is both comprehensive and well-developed (Venables et al., 2016). Based on its success, Venables et al. (2016) recommend the use of similar precautionary management strategies for M. alfredi.

The protection of M. alfredi and its aggregation sites will also ensure protection for many other marine wildlife (Roff & Evans, 2002). Moreover, MPAs may increase resilience to the impacts of climate change (Roberts et al., 2017) by reducing anthropogenic stressors that can increase susceptibility (Cabral, Fonseca, Sousa, & Leal, 2019). For example, increased sea surface temperatures can cause temperature-driven increases in metabolism, thus increasing food requirements (Pistevos, Nagelkerken, Rossi, Olmos, & Connell, 2015). Acclimation is possible via physical or behavioural adaptation (Pistevos et al., 2015); however, human stressors such as organic pollution operate synergistically with increased temperature (Cabral et al., 2019), increasing sensitization (Sokolova & Lannig, 2008) and hindering the animals' ability to adapt (Cabral et al., 2019).

The synergic relationship between human stressors and climate change also threatens coral reefs (Vega Thurber et al., 2014). In the Maldives, deteriorating coral reefs (McClanahan & Muthiga, 2014) require protection to improve reef resilience (Folke et al., 2004). Commitments to the Convention on Biological Diversity Aichi Biodiversity

Targets require the Maldives government to have protected 10% of the nation's coral reef area by 2025 (MEE, 2015). However, currently, the Maldives' 42 MPAs encompass <1% of the reef area (Stevens & Froman, 2018). To meet the 10% target will require the creation of new, much larger MPAs, which encompass and join together key sites of M. alfredi use. For example, immediately outside of the Hanifaru Bay MPA in Baa Atoll are nine key sites used for both feeding and cleaning by adult and juvenile M. alfredi. Expansion of the Hanifaru Bay MPA to encompass all these locations, and merging smaller MPAs into larger areas, would help reduce the impact of anthropogenic stressors, injury, and habitat degradation (Stevens & Froman, 2018). These actions would significantly improve protection for M. alfredi in the Maldives, as well as assist the government achieving its commitments to the Convention on Biological Diversity Aichi Biodiversity Targets. Furthermore, the establishment and maintenance of larger MPAs are more cost effective than smaller MPAs (McCrea-Strub et al., 2011). Currently, due to the absence of management plans and active enforcement at all but one of the Maldives MPAs, they are little more than 'paper parks' that do not offer adequate protection (Mohamed, 2007; Rife, Erisman, Sanchez, & Aburto-Oropeza, 2013). Therefore, the introduction of species- and area-specific management plans for current and future MPAs, and the active enforcement thereof is also required which will greatly assist the protection of M. alfredi and the coral reefs in the Maldives.

To further the current study, future research would benefit from the use of tagging to track M. alfredi movements and identify other key aggregation sites (Stewart, Nuttall, et al., 2018). Site use should also be demographically defined to identify essential requirements for the species reproductive success and overall fitness. Modelling techniques, such as ecological niche factor analysis, could then be used to highlight sites that may be crucial for M. alfredi survivorship. Furthermore, the potential impacts of climate change, such as the weakening of the SW monsoon, should be investigated as a matter of priority.

5 | CONCLUSION

The current study used multiple linear regression and prediction analysis to develop the current understanding of the relationships between M. alfredi seasonal movement in the Maldives and environmental variables. The quantitative evidence presented confirms that M. alfredi movements are predictable both spatially and temporally. While this is advantageous to the tourist economy, the current lack of specific protections for the species throughout the majority of the Maldives archipelago has been shown to lead to direct injury, displacement, and habitat degradation due to anthropogenic stressors. This study identifies how and when sites are most likely to be used by M. alfredi, thus highlighting areas of conservation concern. This knowledge is of particular importance in the face of climate change, providing a clear focus for conservation planning. Of the 48 key aggregation sites identified in the current study, only three fall within an MPA that has a management plan and active enforcement. To alleviate

anthropogenic stressors and prevent injury and displacement of *M. alfredi*, existing MPAs require management, and more areas of key *M. alfredi* habitat require protection. *Mobula alfredi* are an economically important flagship species in the Maldives, thus management plans aimed at safeguarding this species will provide concurrent protection for other vulnerable species and habitats. By anticipating potential adverse impacts to *M. alfredi* at the locations identified in this study, and acting now to mitigate these threats, this species, their habitat, and the tourist industry which depends on them, can be safeguarded.

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