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 monogenic 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 km², which is only 0.5% of the area (21,596 km²) 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 et al., 2011). These images also allow the sex and physical condition of the
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.mantartrust.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-km² 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/m³) 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 $181-359^\circ$ were classified as east, and those within $1-179^\circ$ 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 a month were excluded to reduce the bias a small number of sightings may have on subsequent analysis.

The effect on the total number of $M. alfredi$ sightings 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 1,062 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 $M. alfredi$ sightings 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:

$$|y - \text{mean}(y)|$$

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 six of the aforementioned variables, e.g. $\text{EMAN} \sim$ 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 $\text{EMAN} \sim$ SWWS + ECHLA + monthly SW monsoon wind frequency (the percentage of days each month that the wind direction represented the SW monsoon [202.5–315.5°], 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 ($\text{AIC}_c$) test statistic, which is an asymptotically unbiased estimator of model quality (Burnham & Anderson, 2002). Models are not assessed by the absolute size of $\text{AIC}_c$ but by their relative values over candidate models, particularly the differences between $\text{AIC}_c$ values ($\Delta \text{AIC}_c$) (Burnham & Anderson, 2002). $\Delta \text{AIC}_c$ is calculated using the following form where $i$ is the model:

$$\Delta_i = \text{AIC}_c - \text{AIC}_c^{\text{min}}.$$  

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

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

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

To effectively scale and interpret the $\Delta_i$ values of the chosen models, Akaike weights ($w_{\text{AIC}_c}$) were calculated using the following form where $R$ is the set of models:

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

Therefore, $w_{\text{AIC}_c}$ is relative to the set of chosen models and ranges from 0 (no support) to 1 (complete support). $\text{AIC}_c$, $\Delta \text{AIC}_c$, and $w_{\text{AIC}_c}$ were obtained using the ‘MuMin’ R package (Barton, 2018).

The accuracy of an estimated parameter was inferred from 95% confidence intervals (CIs) for the slope ($\beta$). 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 $\beta$ is averaged across the set of competing models (Burnham & Anderson, 2002).

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

$$\bar{\beta} = \sum_{j=1}^{R} w_j \hat{\beta}_i$$

where $\hat{\beta}_i = 0$ 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

| 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            | Rasdhoo | 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   | Mulid 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 situated on shallow coral reef (≤20 m) of atoll kandus (channels), predominantly 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 different 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 conclusion. 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

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**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).
WMAN was assessed by MLR modelling. Two plausible models within the ΔAICc < 2 threshold were produced (Table 4). The highest-ranking model (W8) with the lowest AICc and the greatest relative weight (ΔAICc = 0, wAICc = 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-α 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: \( \Delta \text{AIC}_c = 0.635, \text{W15}: \Delta \text{AIC}_c = 0.365 \)) but 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

| 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-α | Monthly mean chlorophyll-α concentration on the east side of the atolls. |
| WCHLA        | West Chl-α | Monthly mean chlorophyll-α concentration on the west side of the atolls. |

(WMAN) was assessed by MLR modelling. Two plausible models within the \( \Delta \text{AIC}_c < 2 \) threshold were produced (Table 4). The highest-ranking model (W8) with the lowest AICc and the greatest relative weight (\( \Delta \text{AIC}_c = 0, \text{W8}: \Delta \text{AIC}_c = 0.635 \)) 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-α concentration on the west side of the atolls (WCHLA) reduced WMAN (Figure 4).

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plausible models within the $\Delta$AICc < 2 thresholds were produced (Table 5). Model E15 is the highest-ranking model ($\Delta$AICc = 0, $w_{\text{AICc}} = 0.367$) 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 $\Delta$AICc < 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).
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, 2015, 2011, 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 the 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 five more years (2007, 2009, 2013, 2015, and 2016). 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 (2015, 2008, 2009, 2013, and 2017). For the transition months (March, April, November, and December), predictions were acceptable for two years (2011).

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).

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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 7**  Point estimate of the monthly percentage of manta rays on the east side of the atolls (EMAN) $(y - \text{mean} (y))$ with respective +/− 95% confidence interval of each variable in the east models within the $ΔAIC_c < 2$ 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%)
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 (WB; 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, & Beijder, 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, Elaine, 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, Srivinasan, & Eagle, 2004) and cleaner wrasse activities (Arnal, Kulbicki, Harmelin-Vivien, Galzin, & Morand, 2002; Tiri, Wismer, Leverato, & Bhary, 2018), potentially influencing reef manta ray visitation patterns (Barr & Abelzon, 2019). If disruption of the mutually 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). Semenuk, Bourgeois, Smith, and Rothley (2009) found evidence of this in southern stingrays (Dasyatis 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 tourist 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, Staples, & 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.

ACKNOWLEDGEMENTS

Acknowledgements to the Maldives’ Ministries of Fisheries and the Environment who granted permission to undertake our research. The Maldivian Meteorological Service for accommodating us so quickly with all our data requests. Thank you to Dannielle Su for all your much-appreciated input and of course, thank you to everyone at the Manta Trust who have been of assistance. Finally, thank you to Robert Pethick and Marie and Tony Lang whose support and enthusiasm has made this research possible. This work was supported by the Save Our Seas Foundation who provided grants and enthusiasm has made this research possible. This work was supported by Four Seasons Resorts Maldives at Desroches Island to support multiple aspects of this long-term study throughout its duration. Support was also given by Four Seasons Resorts Maldives, Six Senses Laamu and the Maldives’ Ministries of Fisheries and the Environment.

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REFERENCES

Abish, B., Joseph, P. V., & Johannessen, O. M. (2013). Weakening trend of the tropical easterly jet stream of the boreal summer monsoon season 1950-2009. *Journal of Climate*, 26, 9408–9414. https://doi.org/10.1175/JCLI-D-13-00440.1

Allen, S., Smith, H., Waples, K., & Harcourt, R. (2004). The voluntary code of conduct for dolphin watching in Port Stephens, Australia: Is self-regulation an effective management tool? *Journal of Cetacean Research and Management*, 9, 159–166.

Anderson, R. C., Adam, M. S., & Goes, J. I. (2011). From monsoons to *M. alfredi*: patterns of local distribution of *Manta alfredi* in the Maldives. *Fisheries Oceanography*, 20, 104–113. https://doi.org/10.1111/j.1365-2419.2011.00571.x

Anderson, R. C., Adam, M. S., & Kitchen-Wheeler, A.-M., & Stevens, G. (2010). Extent and Economic Value of Manta Ray Watching in Maldives. *Tourism in Marine Environments*, 7, 15–27. https://doi.org/10.3727/154427310X12867727847973

Armstrong, A. O., Armstrong, A. J., Jaine, F. R. A., Couturier, L. I. E., Flora, K., Uribe-Palomino, J., ... 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, 1–18. https://doi.org/10.1371/journal.pone.0153933

Aram, C., Kulbicki, M., Harmelin-Vivien, M., Galzin, R., & Morand, S. (2002). Patterns of local distribution of *Labroides dimidiatus* in French Polynesian atolls. *Environmental Biology of Fishes*, 63, 9–15. https://doi.org/10.1023/A:1013811205742

Arnold, T. W. (2010). Uninformative Parameters and Model Selection Using Akaike’s Information Criterion. *Journal of Wildlife Management*, 74, 1175–1178. https://doi.org/10.2193/2009-367

Aslam, M., & Kench, P. S. (2017). Reef island dynamics and mechanisms of change in Huvadhoo Atoll, Republic of Maldives, Indian Ocean. *Anthropocene Elsevier B.V.*, 18, 57–68. https://doi.org/10.1016/j.anocene.2017.05.003

Barr, Y., & Abelson, A. (2019). Feeding - cleaning trade-off: Manta ray “Decision-Making” as a conservation tool. *Frontiers in Marine Science*, 6, 1–10. https://doi.org/10.3389/fmars.2019.00088

Barto, K. (2018). Package ‘MuMIn’. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf. [Accessed 5 January 2018]

Braun, C. D., Skomal, G. B., Thorrold, S. R., & Berumen, M. L. (2014). Diving behavior of the reef manta ray links coral reefs with adjacent pelagic habitats. *PLoS ONE*, 9, 1–8. https://doi.org/10.1371/journal.pone.0088170

Brian, A., Venables, B., Bates, D. M., Firth, D. & Ripley, M. B. (2018). Package ‘MASS’. https://cran.r-project.org/web/packages/MASS/MASS.pdf. [Accessed 5 January 2018]

Bruce, J. G., Johnson, D. R., & Kindle, J. C. (1994). Evidence for eddy formation in the eastern Arabian Sea during the northeast monsoon. *Journal of Geophysical Research*, 99, 7651–7664. https://doi.org/10.1029/94JC00035

Burnham, K., & Anderson, D. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. In *Ecological modelling* (2nd ed.). New York: Springer.

Cabral, H., Fonseca, V., Sousa, T., & Leal, M. C. (2019). Synergistic effects of climate change and marine pollution: An overlooked interaction in coastal and estuarine areas. *International Journal of Environmental Research and Public Health*, 16, 1–17. https://doi.org/10.3390/ijerph16152737

Collins, N. (2013). Advocacy for Marine Management: Contributions to a Policy Advocacy Initiative in the Maldives. Capstone Collection. 2608. http://digitalcollections.sit.edu/capstones/2608. [Accessed 20 March 2018]

Côté, I. M. (2000). Evolution and ecology of cleaning symbioses in the sea. In *Oceanography and Marine Biology: An Annual Review* (Vol. 38) (pp. 311–355). London: Taylor & Francis.

Couturier, L. I. E., Jaine, F. R. A., Townsend, K. A., Weeks, S. J., Richardson, A. J., & Bennett, M. B. (2011). Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Krefft, 1868), along the east coast of Australia. *Marine and Freshwater Research*, 628–637. https://doi.org/10.1071/FR101049

Couturier, L. I. E., Marshall, A. D., Jaine, F. R. A., Kashiwagi, T., Pierce, S. J., Townsend, K. A., ... Richardson, A. J. (2012). Biology, ecology and conservation of the *Mobulidae*. *Journal of Fish Biology*, 80, 1075–1119. https://doi.org/10.1111/j.1095-8649.2012.03264.x

Croll, D. A., Dewar, H., Dulvy, N. K., Fernandez, D., Francis, M. P., Galván-Magaña, F., ... White, W. T. (2016). Vulnerabilities and fisheries impacts: The uncertain future of manta and devil rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26, 562–575. https://doi.org/10.1002/aqc.2591

Deakos, M. H., Baker, J. D., & Bejder, L. (2011). Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. *Marine Ecology Progress Series*, 429, 245–260. https://doi.org/10.3354/meps09085

Deik, H., Reuning, L., & Pfeiffer, M. (2017). Orbital scale variation of primary productivity in the central equatorial Indian Ocean (Maldives) during the early Pliocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 480, 33–41. https://doi.org/10.1016/j.palaeo.2017.05.012

DPaW (Department of Parks and Wildlife). (2013). Whale Shark Management with Particular Reference to Ningaloo Marine Park Wildlife Management Program No. 57.

Doty, M., & Oguri, M. S. (1956). The Island Mass Effect. *ICES Journal of Marine Science*, 1, 33–37. https://doi.org/10.1093/icesjms/22.1.33

EPA, Maldives. (2014). Batoidea Maldives Protection Gazette No. (JUL) 438-ECAS/438/2014/81. Ministry of Environment and...
ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environmental Modelling and Software, 25, 1197–1207. https://doi.org/10.1016/j.envsoft.2010.03.029

Roff, J. C., & Evans, S. M. J. (2002). Frameworks for marine conservation - Non-hierarchical approaches and distinctive habitats. Aquatic Conservation: Marine and Freshwater Ecosystems, 12, 635–648. https://doi.org/10.1002/aqc.513

Rohrer, C. A., Pierce, S. J., Marshall, A. D., Weeks, S. J., Bennett, M. B., & Richardson, A. J. (2013). Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. Marine Ecology Progress Series, 482, 153–168. https://doi.org/10.3354/meps10290

Roxy, M. K., Modl, A., Murtugudde, R., Valsala, V., Panickal, S., Prasanna Kumar, S., Levy, M. (2016). A reduction in marine primary productivity driven by rapid warming over the tropical Indian Ocean. Geophysical Research Letters, 43, 826–833. https://doi.org/10.1002/2015GL066979

Roxy, M. K., Ritika, K., Terray, P., Murtugudde, R., Ashok, K., & Goswami, B. N. (2015). Drying of Indian subcontinent by rapid Indian ocean warming and a weakening land-sea thermal gradient. Nature Communications, 6, 1–10. https://doi.org/10.1038/ncomms8423

Sasamal, S. K. (2006). Island mass effect around the Maldives during the monsoon transition. Biogeosciences, 12, 2367–2382. https://doi.org/10.5194/bg-12-2367-2015

Triki, Z., Wismser, L., Levoret, E., & Bshary, R. (2018). A decrease in the abundance and strategic sophistication of cleaner fish after environmental perturbations. Global Change Biology, 24, 481–489. https://doi.org/10.1111/gcb.13943

Turner, A. G., & Annamalai, H. (2012). Climate change and the South Asian summer monsoon. Nature Climate Change, 2, 587–595. https://doi.org/10.1038/nclimate1495

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

Venables, S., McGregor, F., Brain, L., & Van Keulen, M. (2016). Manta ray tourism management, precautionary strategies for a growing industry: A case study from the Ningaloo Marine Park, Western Australia. Pacific Conservation Biology, 22, 295–300. https://doi.org/10.1071/PC16003

Ward-Paige, C. A., Davis, B., & Worm, B. (2013). Global population trends and human use patterns of Manta and Mobula rays. PLoS ONE, 8, 1–9. https://doi.org/10.1371/journal.pone.0074835

White, W. T., Corrigan, S., Yang, L., Henderson, A. C., Bazinet, A. L., Swofford, D. L., & Naylor, G. J. P. (2017). Phylogeny of the manta and devilrays (Chondrichthyes: Mobulidae), with an updated taxonomic arrangement for the family. Zoological Journal of the Linnean Society, 182, 50–75. https://doi.org/10.1093/zoolinnean/zlx018

Yadav, R. K. (2013). Emerging role of Indian ocean on Indian northeast monsoon. Climate Dynamics, 41, 105–116. https://doi.org/10.1007/s00382-012-1637-0

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How to cite this article: Harris JL, McGregor PK, Oates Y, Stevens GMW. Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (Mobula alfredi) in the Maldives, implications for conservation. Aquatic Conserv: Mar Freshw Ecosyst. 2020;1–16. https://doi.org/10.1002/aqc.3350