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The Spatial Ecology of the Reef Manta Ray (*Manta alfredi*) in the Maldives.

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Abstract

The reef manta ray (*Manta alfredi*) is one of the oceans largest planktivores that exist in small subpopulations. Their K-selected life history makes them vulnerable to exploitation, and severe declines mean they are listed as vulnerable to extinction on the IUCN Red List of Threatened Species. The World's largest known population is in the Maldives where they are protected, but effective conservation relies heavily on understanding their spatial ecology. This research furthers a study by Anderson *et al.* (2011a) that identified a biannual east-west migration pattern thought to be driven by peaks in ocean productivity induced by the South Asian Monsoon. This study aims to identify the environmental variables that may be influencing this pattern to establish how they may be affected by climate change. Multiple linear regression and subsequent prediction analysis determined that the southwest monsoon winds and concomitant ocean surface currents are the predominant influence on the monthly proportions of manta rays that are sighted on the east and the west side of the atolls. This knowledge helps to understand the implications that climate change may have on survivorship and provides a baseline for future research to identify the critical migration cues which may assist their ongoing conservation.

Additional keywords: AICc, Information Theoretic, prediction model, elasmobranch, Indian Ocean, Maldivan Manta Ray Project.

Introduction

The reef manta ray (*Manta alfredi*) is a planktivorous elasmobranch that is listed as vulnerable to extinction on the IUCN Red List of Threatened Species (Marshall *et al.*, 2011). They are found circumglobally, bound within tropical and subtropical latitudes (Kitchen-Wheeler, Ari and Edwards, 2012) and exist in small subpopulations (Marshall *et al.*, 2011) that spend their time within a certain range (Rohner *et al.*, 2013). As a K-selected species, overexploitation has led to dramatic declines in some of these populations (Rohner *et al.*, 2013). The world's largest known population exists in the Maldives (Stevens, 2016) thus conservation is crucial. Manta rays are protected in this region, but for conservation to continue to be successful, it is paramount that their spatial ecology and the implications of any possible changes are understood.

The Republic of Maldives is an archipelago in the Indian Ocean made up of 26 coral atolls (Anderson *et al.*, 2011b) which straddle the equator (Kuiter and Godfrey, 2014). The region's meteorology is dominated by intense atmospheric monsoon systems (Anderson *et al.*, 2012) in particular the South Asian Monsoon (SAM) (Stevens, 2016). These systems are closely related to the changes in the thermal contrasts between the land and sea (Sun and Ding, 2011) and the north-south shift of the Intertropical Convergence Zone (ITCZ) (Bruce *et al.*, 1994). This shift can be characterised by a biannual reversal of winds (Betzler *et al.*, 2016) and the concomitant ocean surface currents (Bruce *et al.*, 1994). In the Maldives, these winds drive ocean surface currents across the atolls from west to east during the South West (SW) monsoon and east to west during the North East (NE) monsoon (Anderson *et al.*, 2011a). Turbulence and eddies induced by the topography lead to upwelling on the downstream side of the atolls which brings nutrient-rich waters from depth into the euphotic zone and increases primary productivity (Deik *et al.*, 2017). This enrichment, in turn, supports secondary productivity such as the increase of zooplankton biomass (Gove *et al.*, 2016). This process is known as the Island Mass Effect (Oguri, M. S., Doty, 1956).

The SW monsoon runs from April to November and the NE monsoon from December to March (Schott and McCreary, 2001). The transition period between the monsoons is highly variable which has led to mixed reports as to when it occurs with some suggesting it is April and November (Anderson *et al.*, 2011a; Brown *et al.*, 2017) and others including March and October (Aslam and Kench, 2017).

This environment supports the reef manta ray whose predominant food source is zooplankton which requires energetically efficient foraging strategies that depend on waters with dense assemblages of prey (Goldbogen *et al.*, 2015). Their dependence on this resource is suggested to influence their distribution and migration patterns (Deakos *et al.*, 2011).

In the Maldives, Anderson *et al.* (2011a) obtained information on the seasonal distribution of manta rays from local fishermen and divers. Reports suggested that the manta rays are found on the eastern side of the atolls during the SW monsoon and the western side during the NE monsoon (Anderson *et al.*, 2011a). Evidence suggests that these migrations patterns follow the changes in productivity that occur with the changes in monsoon (Anderson *et al.*, 2011a). Such knowledge has led to the establishment of Marine Protected Areas (MPA) such as Hanifaru Bay MPA where seasonal conditions enhance primary productivity leading to large aggregations of *Manta alfredi* (Stevens, 2016).

Climate change has induced warming of the Indian Ocean basin (Bollasina *et al.*, 2011) which has the potential to disrupt these monsoon cycles (Roxy *et al.*, 2015). While studies have focused on the economic consequences of monsoon disruption (Joseph and Simon, 2005; Turner and Annamalai, 2012) the long-term ramifications for the manta rays has not been explored.

The current study aims to test whether the conclusions by Anderson *et al.* (2011a) are supported by the Maldivan Manta Ray Project (MMPR) database. This database is made up of over 50,000 sightings of *Manta alfredi* that have been individually identified using photo identification techniques (Kitchen-Wheeler, 2010). Spanning a total of 13 years, the data collected by MMRP is not only extensive but, each sighting is rigorously confirmed before its incorporation into the database (Kitchen-Wheeler, 2010) which ensures accuracy. Some of the sightings data has been collected largely to assist in establishing the size of the *Manta alfredi* population in the Maldives (Kitchen-Wheeler, Ari and Edwards, 2012). Consequently, the study sites surveyed were visited at times when the manta rays were most likely to appear to minimise bias in population estimates caused by small samples (Kitchen-Wheeler, Ari and Edwards, 2012). This data collection method could create some bias in the appearance or apparent absence of *Manta alfredi* from a location nonetheless, this dataset is unprecedented and offers

an opportunity to explore their distribution across the Maldives in the most accurate way possible to date.

Furthermore, an information theoretic (IT) approach to multiple linear regression (MLR) modelling is utilised to identify the environmental variables that may be predominantly influencing the reef manta ray's spatial ecology. The variables discerned as most pertinent are then used to predict monthly manta ray proportions on the east and west side of the atolls. These predictions may assist in efficiently optimising management resources, such as enforcement patrols made by rangers, to support conservation efforts. Moreover, it will provide a baseline to asses the possible effects that climate change may have on the spatiotemporal distribution of manta rays in this region.

Based on evidence provided by previous studies, it is hypothesised that the manta ray proportions on the east and west side of the atolls may be influenced predominantly by the SW monsoon winds and NE monsoon winds respectively (Anderson *et al.*, 2011a; Kitchen-Wheeler, Ari and Edwards, 2012) that induce productivity on the downstream side of the atolls (Anderson *et al.*, 2011a).

Materials and Methods

Data Collection

All the following data was obtained for 2005-2017 which was split into a primary sample (2005-2016) for analysis and a hold-out sample (2017) to assess the accuracy of subsequent predictions.

Manta Rays

The current study utilises the Maldivian Manta Ray Project (MMRP) database which includes in excess of 50,000 sightings of more than 4,000 individually identified manta rays from over 250 locations in the Maldives. It has been compiled by researchers, dive operators and citizen science.

Wind

Daily mean wind direction and wind speed data were obtained from the Maldives Meteorological Service, Malé. Monthly wind direction frequency was calculated as the

percentage of days each month that the wind direction represented the NE monsoon (N-E: 0-90°) and the SW monsoon (SSW-NW: 202.5–315°) (Anderson *et al.*, 2011a).

Mean monthly wind frequency was calculated to show the period of each monsoon and identify the months in which transition between the monsoons occurs.

Monthly mean wind speed was calculated from the days that represent the aforementioned NE and SW monsoon wind direction sectors. The remaining days were classified as 'other' and monthly mean wind speed of the days was also calculated.

Calculations were validated using six hourly 10 metre U and V wind component obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim data which were assimilated into ArcGIS 10.5.

Chlorophyll-a Concentrations

Monthly 4km chlorophyll-a (Chl-a) composites were obtained from NASA's Goddard Space Flight Center's Moderate Resolution Imaging Spectroradiometer (MODIS) level 3 (http://oceancolor.gsfc.nasa.gov) and incorporated into ArcGIS. Mean monthly Chl-a concentrations were then extracted from the east (2–6°N and 73.5–76.5°E) and west (2–6°N and 70– 73°E) of the central atolls (Anderson *et al.*, 2011a) using spatial analysis tools.

Data Analysis

Biannual Migration

A map of the Maldives was created in ArcGIS 10.5 including polygons for each of the 26 coral atolls. Each atoll was divided into east and west by first establishing the true centroid of each polygon using calculate geometry (Figure 1). The atoll polygons were then divided into angle segments using Data Management Tools. All the sighting locations were then projected, and those within 1-159° were classified as east and 161-359° were classified as west.
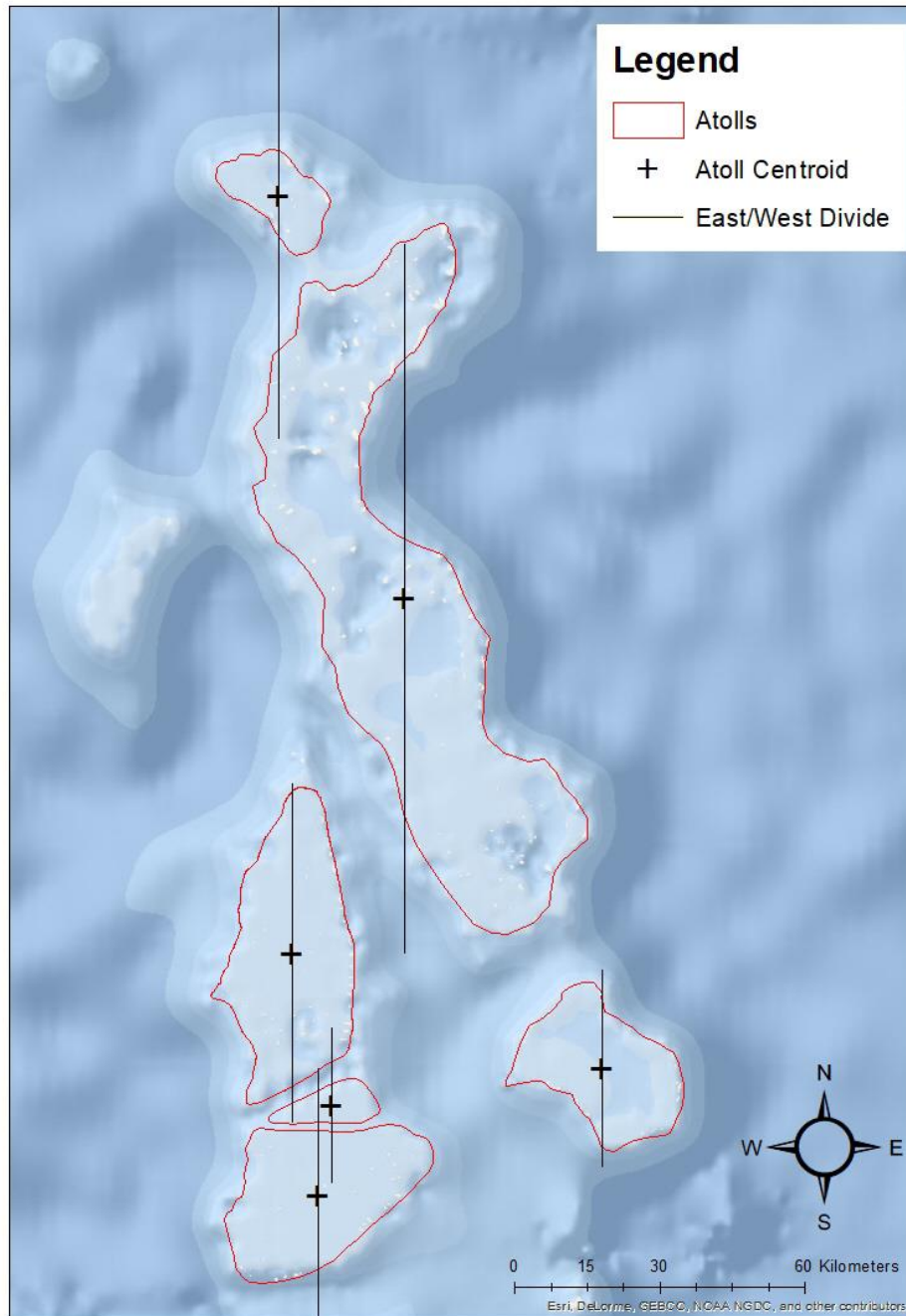
Figure 1 –Example of the east/west classification method showing the Maldives northern atolls with the true centroid of polygons calculated using calculate geometry in ArcGIS and the east/west divide that was established.

All sightings between 2005-2016 were then integrated and projected as monthly total sightings at each location. Any locations with <5 sightings in one month were excluded to reduce the bias a small number of sighting may have on subsequent analysis.

A two-way analysis of variance (ANOVA) was then applied in R 3.4.2 to the total number of manta rays ($log^{10}(y+1)$) observed on the east and west side of the atolls during the SW and NE monsoons.

Environmental Influences

Spearman's Rank correlation analysis was performed in R as an initial assessment of the relationship between all the variables considered in the current study.

Multiple linear regression (MLR) modelling was used to explore the influence of environmental variables on the manta ray's migration pattern using the primary sample. The response variable is the monthly proportion (%) of manta rays observed on the east or the west side of the atolls which were transformed to their difference from the mean, ignoring the sign of difference using the following form:

$$\Big(abs\big(y - mean(y)\big)\Big)$$

East and west were modelled independently including six explanatory variables: monthly percentage of days the wind direction represented the NE and SW monsoons, mean monthly wind speed of NE and SW monsoon winds, wind speed for the days that winds did not represent either NE or SW monsoon ('other') and mean monthly Chl-a concentration on the west side of the atolls for the west models and east side for the east models.

Regsubsets of the 'leaps' R package (Lumley, 2017) was used to determine the order of incorporation of these variables. An assessment of autocorrelation was made by visual inspection of the autocorrelation function (ACF) plot of residuals, followed by a Durbin-Watson test (Crawley, 2013) from the 'lmtest' library (Millo and Mitchell, 2017). Models that did not meet the requirements of the Durbin-Watson test (Field, Miles and 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 and Slate, 2006). Models that did not satisfy all assumptions were also excluded from analysis.

An information theoretic (IT) approach was adopted as an alternative to the conventional hypothesis testing using a single null model (Burnham and Anderson,

2002; Grueber *et al.*, 2011). The IT approach permits several competing hypotheses to be tested simultaneously by ranking and weighting models to provide a quantitative measure of relative support (Grueber *et al.*, 2011) thus allowing some inferences to be made about other models (Burnham and Anderson, 2002).

Rank was established using Akaike's Information Criterion (AIC) test statistic which is an estimated measure of model quality (Burnham and Anderson, 2002) used as an asymptotically unbiased estimator of information to assist in discriminating between competing statistical models (Hurvich and Tsai, 1991). The corrected AIC (AICc) is an adjusted AIC that includes greater penalty for the number of parameters included in the model, therefore, improving the bias properties (Hurvich and Tsai, 1991). Burnham and Anderson (2002) recommend the use of AICc as standard thus it was chosen as the IT criteria for the current study.

Models are not assessed by absolute size of AICc but by their relative values over candidate models, particularly the differences between AICc values (ΔAICc) (Burnham and Anderson, 2002). ΔAICc 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 ΔAICc <2 are considered to have substantial support, models with 4-7 ΔAICc have considerably less, and those with ΔAICc >10 have essentially none (Burnham and Anderson, 2002). Plausible models for the current study were identified as those with ΔAICc <2 and all other models were excluded from 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 (wAICc) was 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 (Kamil Bartoń, 2018).

Multi-model inference should include the evaluation of 95% confidence intervals (CI) and model averaging if the highest ranking model has $_{w}$AIC$_{c}$ <0.9 (Arnold, 2010) and where models within $_{\Delta}$AIC$_{c}$<2 of the top model differ by only one parameter as the larger model is not really supported or competitive (Burnham and Anderson, 2002).

The accuracy of an estimated parameter may be inferred from 95% CI range whereby a narrower range implies a more precise estimation (Beaujean, 2014) while a slope (β) that does not span zero indicates that the null hypothesis may be rejected (Abdi, 2003). For the current study, CI was calculated using the R package 'MASS' (Brian *et al.*, 2018).

Model averaging assists in multi-model inference (Burnham and Anderson, 2002) based on the evidence from all of the plausible models (Hamra, Kaufman and Vahratian, 2015) and helps to 'ameliorate the effect of uninformative parameters' (Arnold, 2010). Model averaging using the full-model averaging approach (Symonds and Moussalli, 2011) was conducted using the 'Mumin' R package (Kamil Bartoń, 2018) whereby the β is averaged across the set of competing models (Grueber *et al.*, 2011).

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 and Anderson, 2002).

Predictive Models

The environmental variables of the most plausible model(s) identified through MLR were used to predict monthly manta ray proportions on the east and the west side of the atolls utilising the predict() function of the R 'stats' package (R Core Team, 2013). The prediction parameters were set using the environmental variables from the hold-out samples and accuracy of predictions was assessed by comparing the results to the MMRP sightings data 2017.

Acceptable error margins for the difference between the predicted and actual monthly proportions of manta rays on the east and west side of the atolls were set whereby <15% = accurate, 15-20% = acceptable, >20% = inaccurate.

A Wilcoxon signed rank test was then applied to assess whether the overall difference between predicted and actual proportions of manta rays on the east and the west side of the atolls was significant.

Results

Wind

Mean wind direction frequency indicates that that the SW monsoon occurs from April until November and the NE monsoon runs from December to March. The transition months appear to November/December between the SW and NE monsoon and March/April between the NE and SW monsoon.
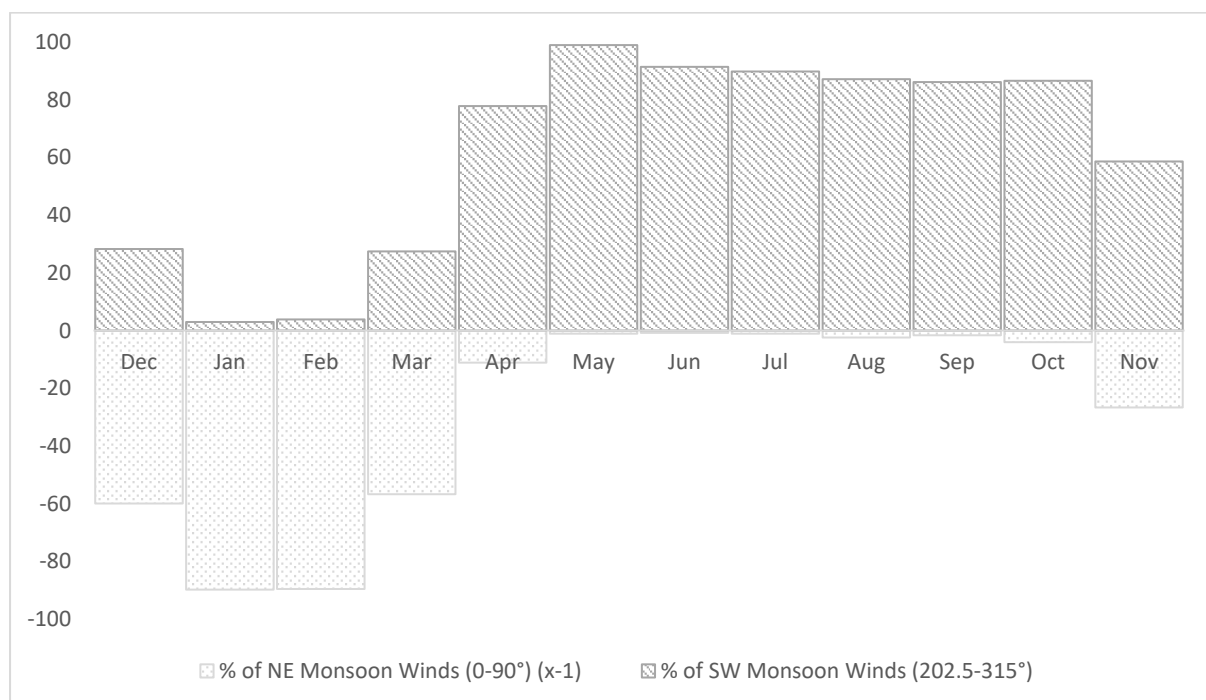
Figure 2 - Mean monthly wind direction frequency 2005-2016 using the rages identified by Anderson (NE = 0-90° SW=202.5-315°). NE monsoon wind frequency is transformed (χ^*-1) to accentuate the monthly variations. Transitional months appear to be November/December, March/April but, based on wind direction frequency, April and November are predominantly SW monsoon while March and December are predominantly NE monsoon.

Biannual Migration

The spatiotemporal variation in the proportion of manta rays visualised in ArcGIS (Figure 3) supports the biannual east-west migration pattern reported by Anderson *et al.* (2011a).
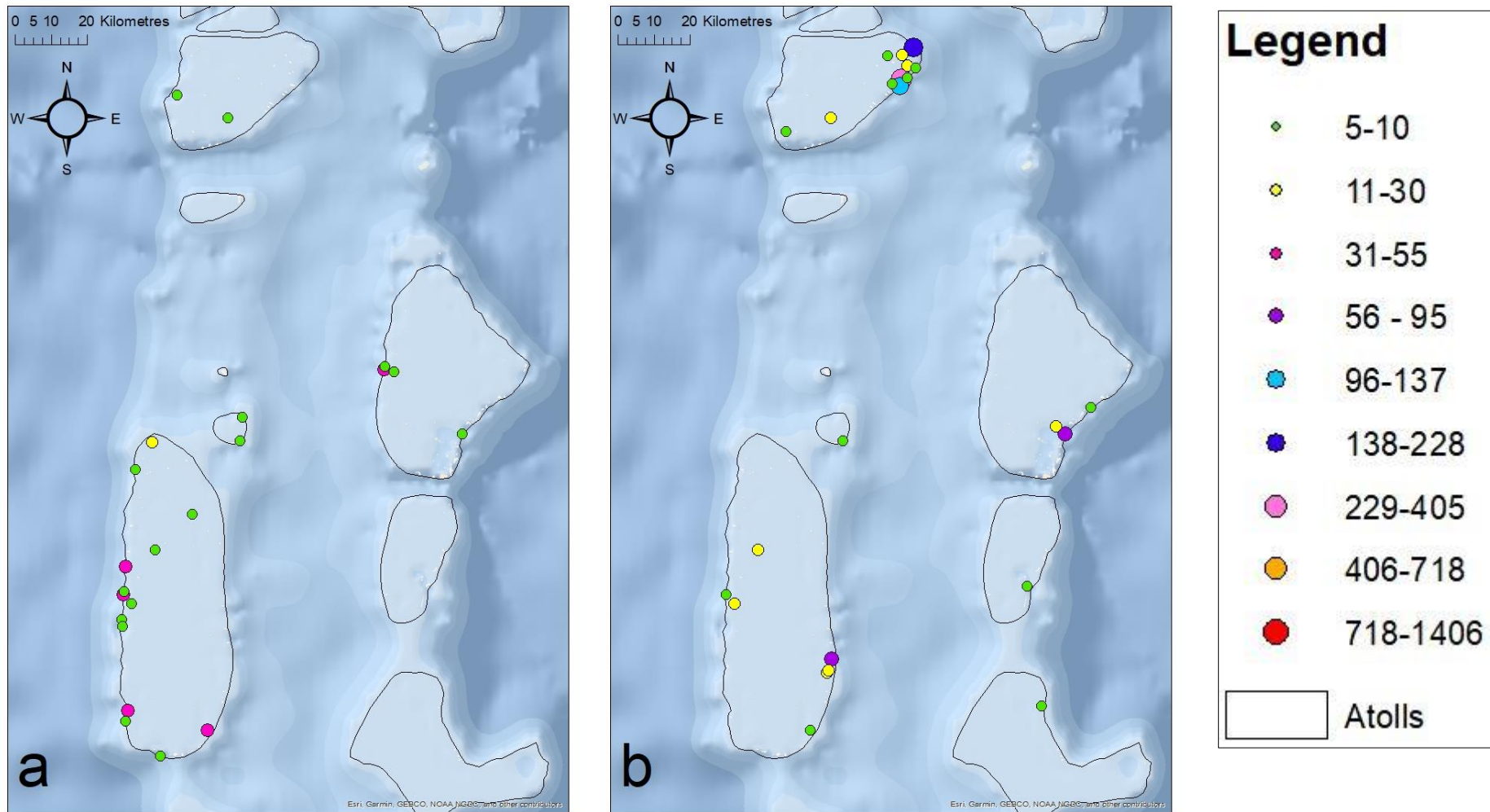
Figure 3 – Example of ArcGIS projection of the monthly total number of manta rays seen on the east and west of the atolls showing the north-central chain of atolls during the (a) NE monsoon using January 2015 when manta rays are predominantly on the west (b) SW monsoon using September 2015 when manta rays are predominantly on the east.

A two-way ANOVA applied to the total number of manta rays ($log^{10}(y + 1)$) observed on the east and west of atolls during the SW and NE monsoon provides evidence that the pattern is not random, with a signficant interaction effect between the side of the atolls and the monsoon period ($F_{1, 44}$ = 55.59, *p*<<0.001).

Environmental Influences

The abbreviations and description of all the variables considered in the current study are shown in Table 1

Table 1 - Abbreviations and description of the variables.

Abbreviation	Variable	Variable description
EMAN	East manta rays	Monthly proportion (%) of manta rays on the east of the atolls.
WMAN	West manta rays	Monthly proportion (%) of manta rays on the west of the atolls.
WDSW	Wind direction southwest	Monthly southwest monsoon wind frequency
SWWS	Southwest wind speed	Monthly mean southwest monsoon wind speed.
WDNE	Wind direction northeast	Monthly northeast monsoon wind frequency.
NEWS	Northeast wind speed	Monthly mean northeast monsoon wind speed.
OTSW	Other wind speed	Monthly mean wind speed of 'other' directions.
ECHLA	East Chl-a	Monthly mean Chl-a concentration on the east side of the atolls.
WCHLA	West Chl-a	Monthly mean Chl-a concentration on the west side of the atolls.

The results of the Spearman's Rank correlation analysis displayed in Figure 4 indicates that the manta ray proportions on the east side of the atolls (EMAN) are positively correlated to SWWS (r_s = 0.503, p<<0.001) and WDSW (r_s = 0.587, p<<0.001) and negatively correlated with NEWS (r_s = -0.562, p<<0.001), WDNE (r_s = -0.626, p<<0.001) and WCHLA (r_s = -0.499, p<<0.001). The correlation of these variables with the proportions of manta rays on the west side (WMAN) of the atolls is inverse; SWWS (r_s = -0.541, p<<0.001), WDSW (r_s = -0.597, p<<0.001), NEWS (r_s = 0.518, p<<0.001), WDNE (r_s = 0.611, p<<0.001) and WCHLA (r_s = 0.432, p<<0.001). ECHLA has a negative correlation with WMAN (r_s = -0.173, p<0.05) but no significant correlation with EMAN.
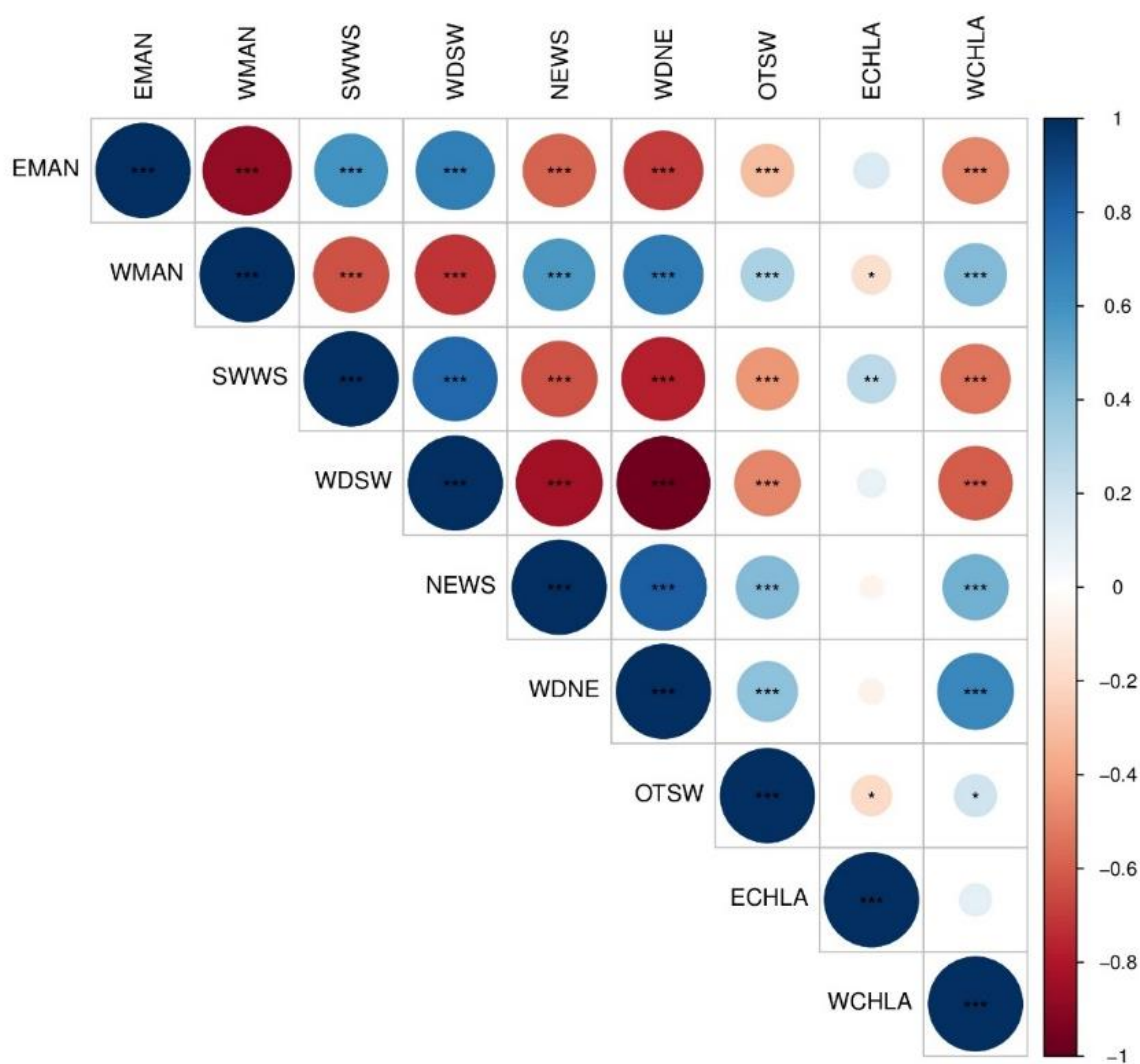
Figure 4 - Spearman's Rank correlation matrix displaying the relationship between all variables (Significance level = *<0.01, **<0.01, *<0.05).

MLR modelling of WMAN produced three plausible models within the $\Delta AIC_c<2$ threshold (Table 2). The 'top model' (W8) with the lowest AIC_c and the greatest relative weight ($\Delta AIC_c = 0$, $wAIC_c = 0.568$) suggests WDSW + SWWS is the predominant influence on WMAN ($F_{2,138} = 29.52$, $R^2 = 0.29$, $p<<0.001$).

Table 2 - Multiple linear regression results of plausible models ($\Delta AIC_c<2$) where the response variable is the monthly proportion of manta rays on the west side of the atolls (WMAN).

Name	Model	df	AICc	ΔAICc	wAICc (ΔAICc <2)	R²	p-value	F-value
W8	SWWS+WDSW	4	-156.4405	0	0.568	0.29	<<0.001	$_{2,138}$ 29.52
W17	SWWS+WDSW+WCHLA	5	-154.5383	1.9	0.219	0.29	<<0.001	$_{3,137}$ 19.65
W16	SWWS+WDSW+WDNE	5	-154.4727	1.97	0.212	0.28	<<0.001	$_{3,137}$ 19.62
W0	NULL	2	-110.4254	46.02	0	n/a	n/a	n/a

West models within the $\Delta AIC_c<2$ thresholds have little ambivalence with all indicating that SWWS and WDSW are influential variables (Table 2). The additional variables in model W17 and W16 are WCHLA and WDNE respectively. Model W17 appears to explain the same amount of variation in WMAN as the top model (W8) ($F_{3,137} = 19.65$, $R^2 = 0.29$, $p<<0.001$) which indicates that WCHLA does not explain any more of the variation than SWWS+WDSW alone. Similarly, the addition of WDNE (W16) also does not improve the model ($F_{3,137} = 19.62$, $R^2 = 0.28$, $p<<0.001$). The $wAIC_c$ of all three models supports this inference as model W17 and W16 hold considerably less weight than the top model (W8 - $wAIC_c = 0.568$, W17 - $wAIC_c = 0.219$, W16 - $wAIC_c = 0.212$).

Figure 5 depicts the CI for the explanatory variables of each of the models and the averaged model. The CI for SWWS is consistent throughout the models and has the narrowest range which implies it is the most precisely estimated parameter (Beaujean, 2014). In model W8 the β for the estimate of both SWWS and WDSW does not span zero which indicates that the null hypothesis may be rejected however, due to the wider CI, WDSW may be a less precise estimator.
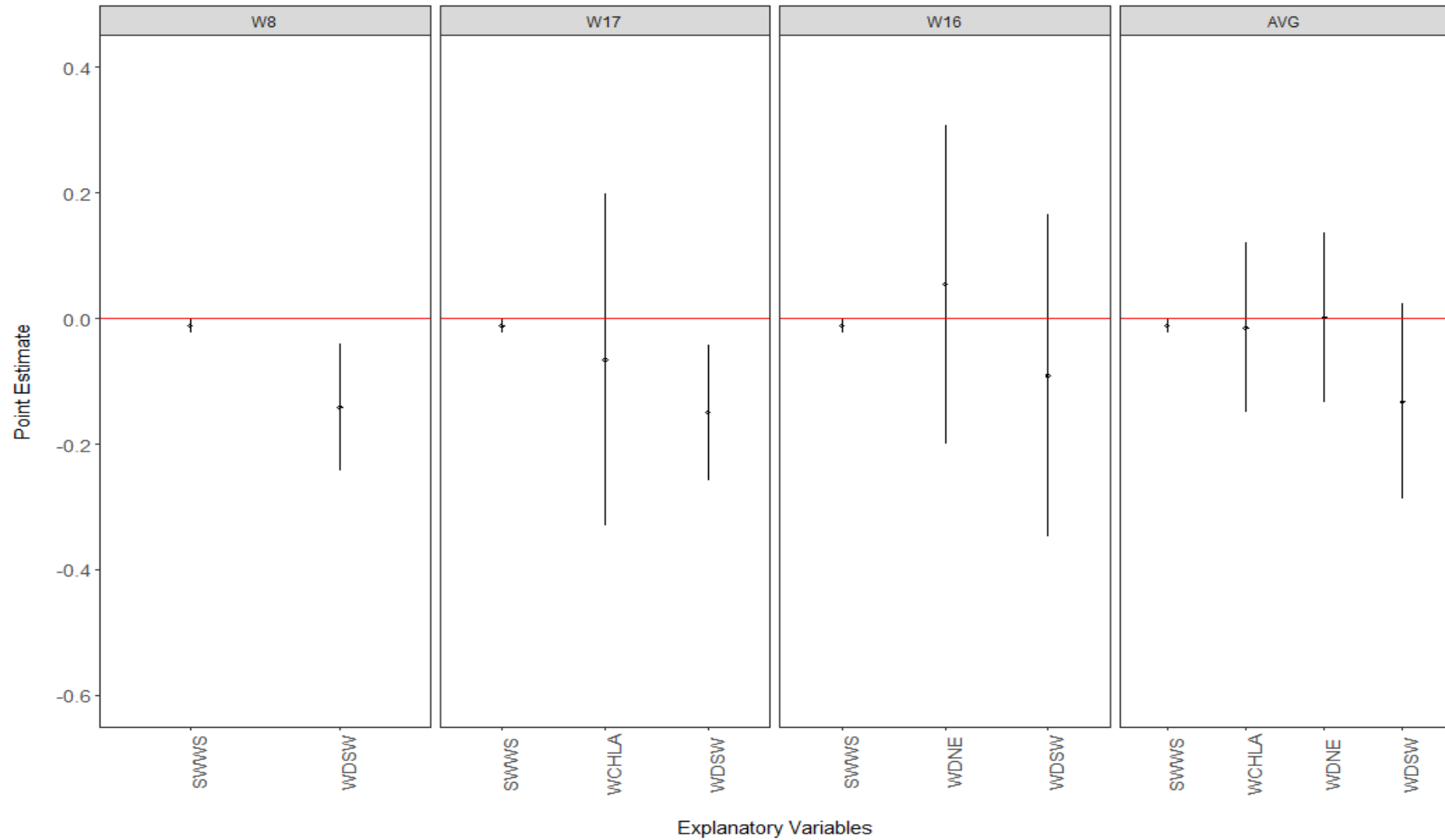
Figure 5 - Point estimate of WMAN $\left(abs(y - mean(y))\right)$ with respective +/- 95% CI of each variable in the west models within the $_\Delta$AIC$_c$<2 threshold. Variable abbreviations and descriptions are given in Table 1.

Model averaging does not adjust the CI of SWWS indicating it is a useful parameter (Arnold, 2010) however, WDSW varies from model to model. It is suggested that the change in CI for WDSW in model W16 is due to the influence of the additional variable, WDNE. Both WDNE and WCHLA appear with SWWS+WDSW in lower ranking models, and both have wide CI intervals with β that span zero, therefore suggesting that they are not significant variables (Arnold, 2010). In the averaged model WDSW has a wide CI and β spans zero (-0.288, 0.023) suggesting it may not be a reliable estimator, however, it is suggested that this is due to the influence of the additional variables in W17 (WCHLA) and W16 (WDNE), which have been identified as unreliable parameters (Burnham and Anderson, 2002; Arnold, 2010), thus these models may be rejected. After excluding WCHLA and WDNE, model W8 is suggested to be the most plausible model to explain variation in WMAN.

MLR modelling of EMAN produced eight plausible models within the $\Delta AIC_c < 2$ thresholds (Table 3).

Table 3 - Multiple linear regression results of plausible models ($\Delta AIC_c < 2$) where the response variable is the monthly proportion of manta rays on the east side of the atolls (EMAN).

Name	Model	df	AICc	ΔAICc	wAICc (ΔAICc <2)	R²	*p*-value	*F*-value
E8	SWWS+WDNE	4	-154.4065	0	0.204	0.15	<<0.001	$_{2,138}$ 13.21
E2	WDNE	3	-153.9328	0.47	0.161	0.14	<<0.001	$_{1,139}$ 23.59
E10	SWWS+WDSW	4	-153.6529	0.75	0.14	0.14	<<0.001	$_{2,138}$ 12.77
E13	SWWS+NEWS	4	-153.2749	1.13	0.116	0.14	<<0.001	$_{2,138}$ 12.55
E1	WDSW	3	-153.065	1.34	0.104	0.13	<<0.001	$_{1,139}$ 22.59
E3	SWWS	3	-153.0392	1.37	0.103	0.13	<<0.001	$_{1,139}$ 22.56
E6	ECHLA+WDNE	4	-152.8348	1.57	0.093	0.14	<<0.001	$_{2,138}$ 12.3
E17	SWWS+ECHLA+WDNE	5	-152.5207	1.89	0.079	0.14	<<0.001	$_{3,137}$ 8.843
E0	Null	2	-133.9192	20.49	0	n/a	n/a	n/a

E8 is suggested to be the 'top model' ($\Delta AIC_c = 0$, $_wAIC_c = 0.204$) which is estimated to explain 15% of the variation in EMAN ($F_{2,138} = 13.21$, $R^2 = 0.15$, $p<<0.001$) however, the weight of E8 is relatively low and all competing models have similar weights. Multi-model inference via CI (Figure 6) provides evidence that all the explanatory variables except WDNE in model E2 and E6 and WDSW in model E1 may be unreliable estimators of EMAN as all β span zero.
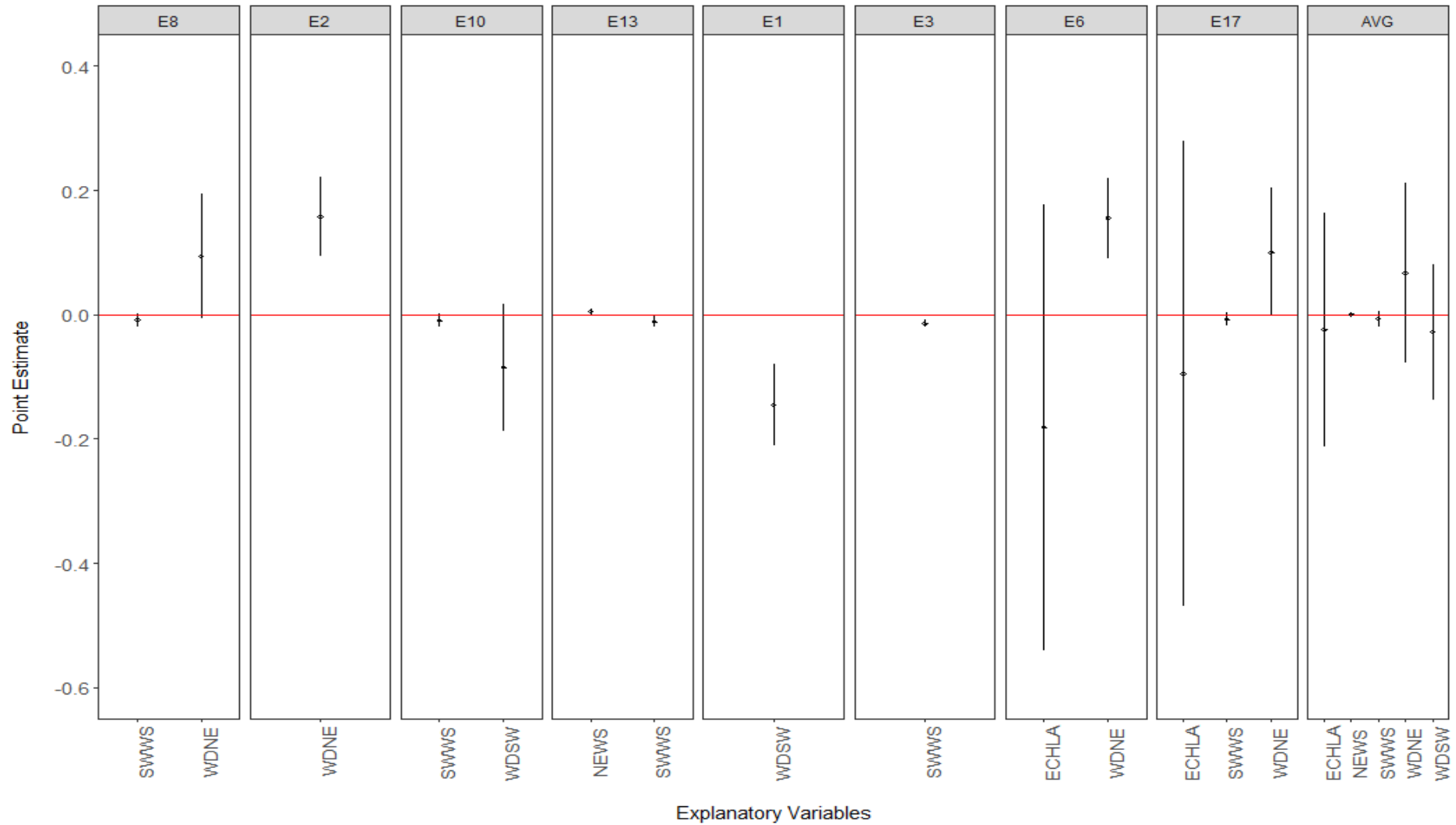
Figure 6 - Point estimate EMAN $\left(abs(y - mean(y))\right)$ with respective +/- 95% CI of each variable in the east models within the $\Delta AIC_c < 2$ threshold. Variable abbreviations and descriptions are given in Table 1.

The CI of WDNE in model E2 suggests it is a significant variable. The addition of SWWS in model E8 appears to improve the model based on $_\Delta$AIC$_c$ and $_w$AIC$_c$, but the null hypotheses for both variables in E8 cannot be rejected thus E2 may be considered a more plausible model. Model averaging (Figure 6), applied to minimise the effects of uninformative parameters (Arnold, 2010), provides evidence that the null hypothesis may not be rejected for any of the variables. ECHLA may be the most negligible estimator due to its wide CI making it unlikely to closely estimate EMAN which indicates model uncertainty for any model containing this variable. Furthermore, ECHLA in model E6 and E17 is an additional parameter to those found in higher ranking models E8 and E2. Therefore, ECHLA does not appear to increase the explanatory power of the models (Table 3) thus models with ECHLA may be eliminated from further analysis. Overall, models E8, E2, E10, E13, E1 and E3 all have significant standing and may serve equally well in approximating EMAN.

Prediction Models

MLR modelling and subsequent analysis for the west side of the atolls suggests that there is a single 'top-model' (W8) that included the variables SWWS+WDSW. The predictions calculated with these variables using the predict() function in R are displayed in Table 4 and Figure 7.

Table 4 – WMAN calculated from MMRP hold-out sample compared to the predictions calculated by predict() function of the R 'stats' package using the variables identified by model W8 and mean error margin.

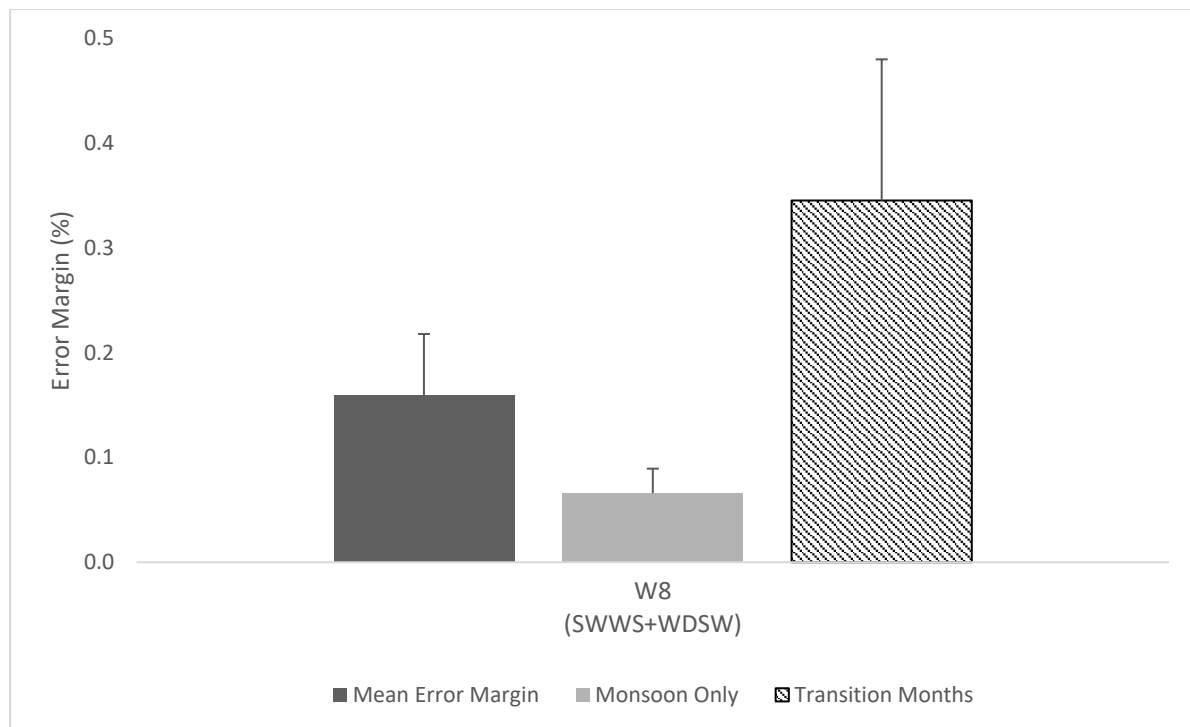| Month	WMAN (MMRP - 2017)	W8 Prediction (SWWS+WDSW)	Difference
Jan	0.8206	0.8540	0.0334
Feb	0.9289	0.7264	0.2024
Mar	0.9478	0.4919	0.4559
Apr	0.7241	0.0653	0.6589
May	0.0882	0.0111	0.0771
Jun	0.0566	0.0786	0.0220
Jul	0.0062	0.1293	0.1231
Aug	0.0428	0.0583	0.0154
Sep	0.0040	0.0228	0.0189
Oct	0.0117	0.0468	0.0351
Nov	0.3175	0.2774	0.0401
Dec	0.7280	0.5018	0.2262
		Mean Error Margin	0.1590

Figure 7 –   Percentage difference between WMAN (MMRP 2017) compared to the predictions calculated by predict() function of the R 'stats' package using the variables identified by model W8. Showing overall mean error margin, the error margin of the monsoon only months (January, February, May-October) and the error margin of the transition months only (March, April, November and December) all with +SE.

The mean error margin between the predicted WMAN and the actual percentage calculated from MMRP hold-out sample was 15.9%. Seven out of the 12 months were predicted within a 15% (accurate) error margin while February (error = 20.2%) and December (error = 22.6%) were just above the 20% (inaccurate) threshold. March and April were not accurately predicted by the variables identified by model W8.

A Wilcoxon signed rank test showed that, overall, there was no significant difference between the predicted WMAN and the MMRP hold-out sample ($Z = 0.266$, $p>0.05$).

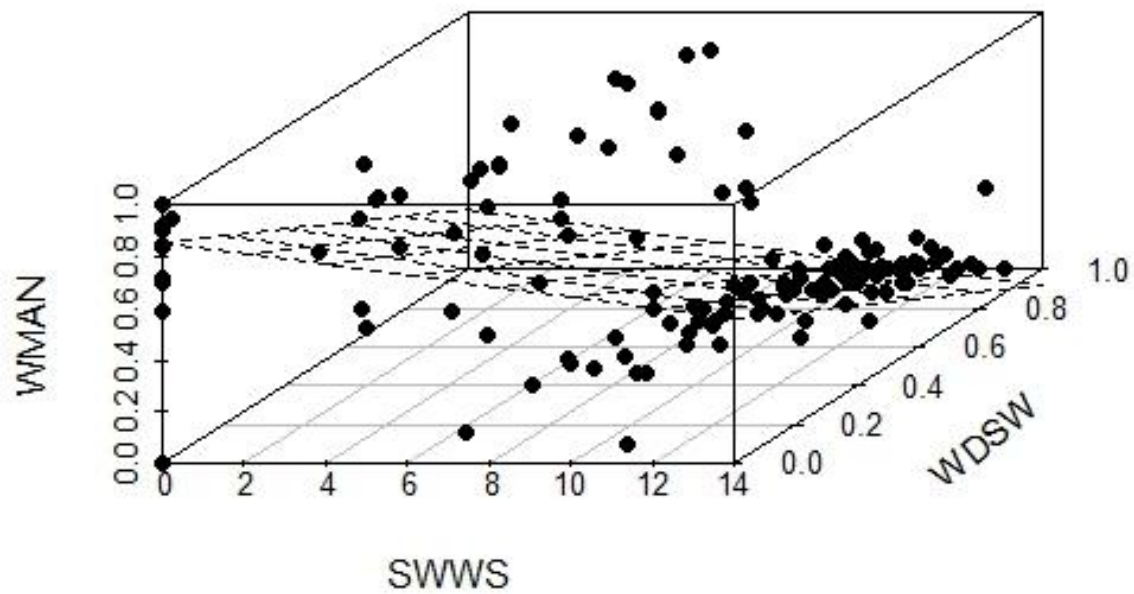Figure 8 depicts the relationship between WMAN and SWWS+WDSW. Both SWWS and WDSW have a negative influence on WMAN.

Figure 8 –Relationship between WMAN and the variables identified by model W8 (SWWS+WDSW) with regression plane of best fit to data points suggesting SWWS and WDSW has a negative influence on WMAN.

For the east side of the atolls, MLR and subsequent CI and model averaging analysis identified six plausible models (E8, E2, E10, E13, E1 and E3). A summary of the results from the predictions based on the variables of these models is shown in Figure 9.
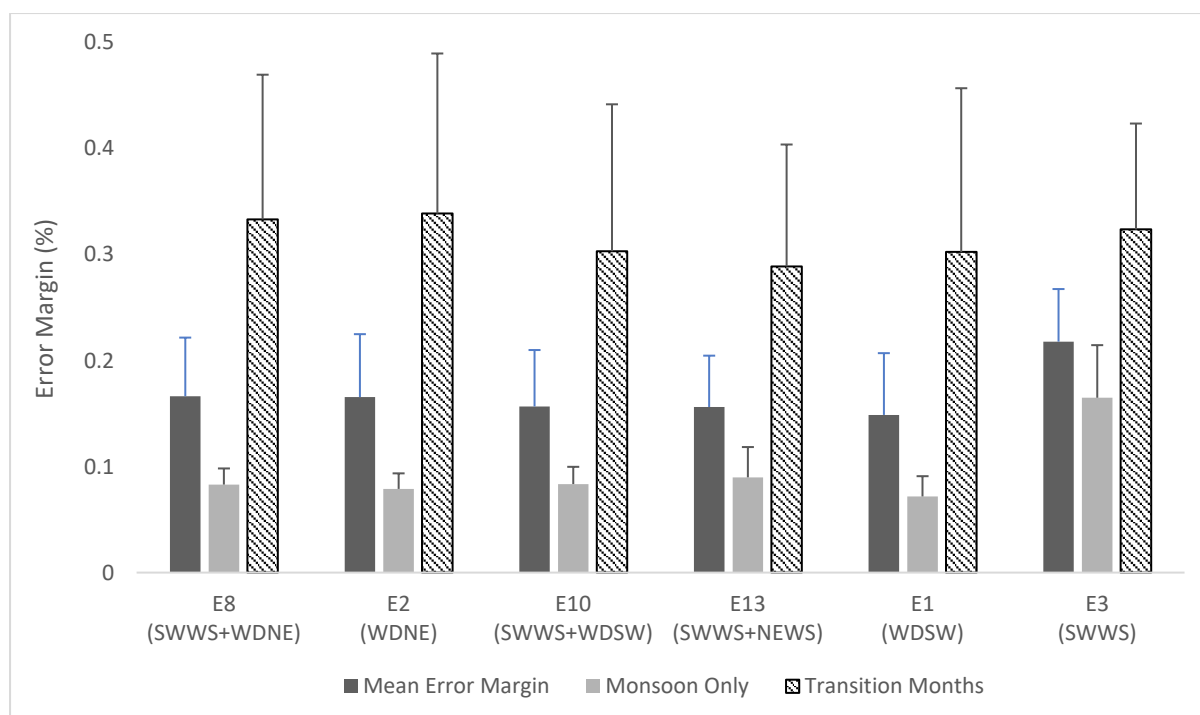
Figure 9 – Percentage difference between EMAN hold-out sample (MMRP 2017) and the predictions calculated by predict() function of the R 'stats' package using the variables identified by models E8, E2, E10, E13, E1 and E3 (variables shown in brackets). Showing overall mean error margin, the error margin of the monsoon only months (January, February, May-October) and the error margin of the transition months only (March, April, November and December) all with +SE.

A Wilcoxon Signed-rank test applied to the results of the predictions of each of the variables or combination of variables identified by each model suggests there is no significant difference ($p > 0.05$) between any of the predicted EMAN and those calculated from the MMRP hold-out sample.

Of all six models, the predictions made by the variable identified by model E1 (WDSW) shown in Table 5 and Figure 9 had the lowest mean error margin (14.8%). A total of 10 months were predicted accurately (error<15%) which included November (error = 0.3%) and December (error = 9.5%) but this model failed to predict March (error = 44.1%) and April (error = 66.9%) with highest error margin for these months of any of the models. Model E3 (Table 6 and Figure 9) had the least predictive success with a mean error margin of 21.7% with the highest error occurring in December (error = 47.8%), but this model has the lowest error margin for March (error = 39.9%) and April (error = 39.5%).

Table 5 – EMAN calculated from MMRP hold-out sample compared to the predictions calculated by predict() function of the R 'stats' package using the variables identified by model E1 (WDSW) and mean error margin.

Month	EMAN (MMRP - 2017)	E1 Prediction (WDSW)	Difference
Jan	0.1794	0.1669	0.0125
Feb	0.0711	0.1947	0.1236
Mar	0.0522	0.4933	0.4411
Apr	0.2759	0.9453	0.6694
May	0.9118	0.9202	0.0084
Jun	0.9434	0.9193	0.0241
Jul	0.9938	0.8699	0.1238
Aug	0.9572	0.8951	0.0621
Sep	0.9960	0.9193	0.0767
Oct	0.9883	0.8448	0.1434
Nov	0.6825	0.6858	0.0033
Dec	0.2720	0.3678	0.0957
		Mean Error Margin	0.1487

Table 6 – EMAN calculated from MMRP hold-out sample compared to the predictions calculated by predict() function of the R 'stats' package using the variables identified by model E3 (SWWS) and mean error margin.

Month	EMAN (MMRP - 2017)	E3 Prediction (SWWS)	Difference
Jan	0.1794	0.0911	0.0883
Feb	0.0711	0.4530	0.3819
Mar	0.0522	0.4426	0.3903
Apr	0.2759	0.6718	0.3960
May	0.9118	0.9251	0.0133
Jun	0.9434	0.6969	0.2465
Jul	0.9938	0.6577	0.3360
Aug	0.9572	0.8323	0.1249
Sep	0.9960	0.8874	0.1087
Oct	0.9883	1.0078	0.0195
Nov	0.6825	0.6522	0.0303
Dec	0.2720	0.7501	0.4780
	Mean Error Margin		0.2178

Figure 10 shows the estimated relationship between EMAN and the most accurate predictor variable WDSW which suggests WDSW have a positive influence on EMAN.
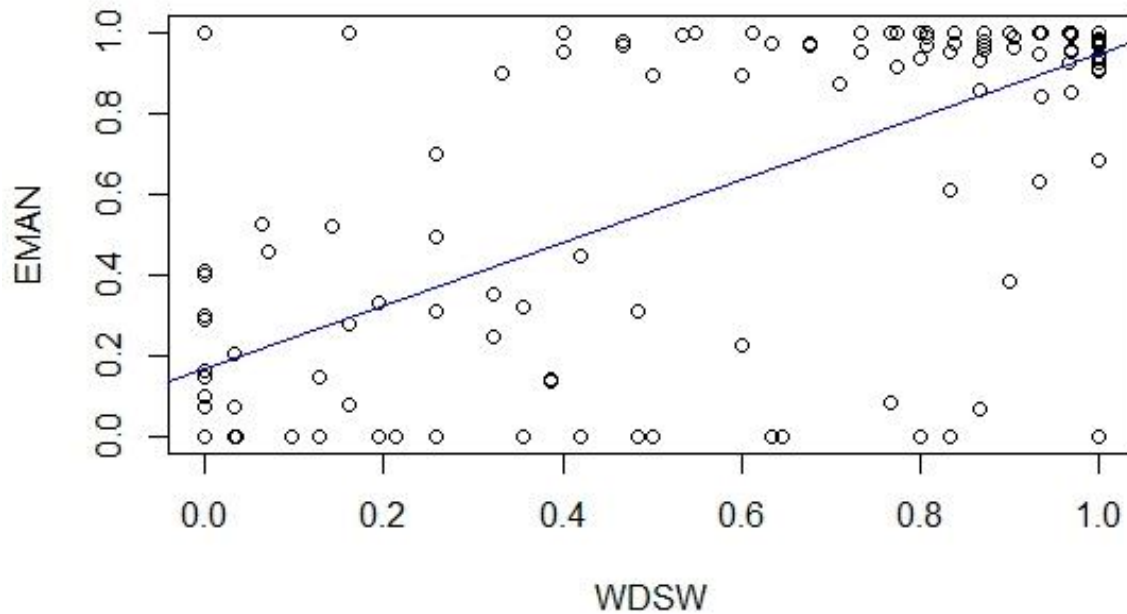
Figure 10 – Relationship between EMAN and the most accurate predictor variable WDSW with linear regression line of best fit to data points suggesting WDSW has a positive influence on EMAN.

Discussion

The biannual east-west migration pattern of manta rays in the Maldives is not a newly discovered phenomenon. Knowledge of these migration patterns and seasonal aggregation sites has been utilised by fishermen and the tourist economy for many years (Anderson *et al.*, 2011a).

The seasonal aggregations of planktivorous marine megafauna such as *Manta alfredi* have been linked to their need for energy efficient foraging strategies (Goldbogen *et al., 2015)*. These strategies rely on dense assemblages of zooplankton (Goldbogen *et al.*, 2015), a resource that exhibits spatiotemporal fluctuations influenced by a variety of biotic and abiotic factors (Armstrong *et al.*, 2016).

The seasonal upwelling phenomenon in the Maldives, induced by the biannual reversal of monsoon winds (Deik *et al.*, 2017) and the Island Mass Effect (Sasamal, 2006) triggers phytoplankton blooms and in turn increases zooplankton biomass (Elliott *et al.*, 2012). This understanding has been crucial for conservation in the region, for example, the development of protected areas such as Hanifaru Bay MPA.

In 2011, the biannual east-west migration of *Manta alfredi* was clarified by Anderson *et al.* (2011a) using anecdotally gleaned data from local fishermen and divers. Through quantitative analysis of the MMRP database utilising ArcGIS and R, the current study provides further evidence to support the conclusions of Anderson *et al.* (2011a). This result was expected based on previous studies that report the occurrence of manta rays on the west side of the atolls during the NE monsoon and east of the atolls during the SW monsoon (Anderson *et al.*, 2011a; Kitchen-Wheeler, Ari and Edwards, 2012). However, the predominant influence of this migration pattern had not been identified although it is implied to be the corresponding monsoons and peaks in primary productivity (Anderson *et al.*, 2011a).

The results of Spearman's rank correlation tests provide evidence to support this implied association with the monsoon winds. With the exception of the monthly proportion of manta rays on the east side of the atolls (EMAN) and monthly mean Chl-a on the east side of the atolls (ECHLA), productivity was found to correlate to manta proportions. The lack of correlation between EMAN and ECHLA may be due to the method used to establish mean Chl-a concentration. Peaks in Chl-a occur on the east side of the atolls during the SW monsoon, but this is a time when cloud cover is greatest. Increased cloud cover obscures Chl-a which could generate inaccurate null values in pixels used in ArcGIS to calculate the mean concentration. This impediment has been highlighted in other studies (Sequeira *et al.*, 2014; Weeks *et al.*, 2015). Furthermore, the spatial resolution of composites may have led to small areas of variation being lost (Moses *et al.*, 2009) which may have confounded the results. Alternatively, Chl-a may not be a reliable measure of primary productivity because although Chl-a is found to correlate to phytoplankton (Jaine *et al.*, 2012) whereby high levels of Chl-a indicate a bloom, low concentrations do not preclude bloom activity (Livingston, 2005).

The assessment of the influence of environmental variables on EMAN and manta ray proportions on the west side of the atolls (WMAN) were further developed using an IT approach to MLR modelling. Evidence presented estimates that there may not be a significant relationship between mean Chl-a and EMAN or WMAN. As well as the aforementioned confounding factors associated with ECHLA, there may be other reasons why ECHLA and monthly mean Chl-a on the west side of the atolls (WCHLA) were found not to be significantly influential. For example, manta rays are only

affiliated with peaks in phytoplankton because phytoplankton is associated with zooplankton blooms, but this succession is subject to a temporal lag (Jaine *et al.*, 2012) which was not taken into account in the current study. Moreover, peaks in phytoplankton could also indicate a reduction in zooplankton biomass due to reduced grazing pressure (Cury *et al.,* 2015) which may reduce EMAN and WMAN.

The overall accuracy of the prediction results provides evidence that dominant influence on EMAN and WMAN is the SW monsoon winds. The importance of the winds that are associated with SW monsoon that occur during the NE monsoon may be understood through the assessment of the monthly prediction accuracy. Monthly predictions for both the east and the west side of the atolls indicate that the transition months between the NE and SW monsoon (March and April) and the SW and NE monsoon (December) are the most difficult to predict. Although referred to as transition months, they are better described as the onset and retreat of the SW monsoon (Charlotte *et al.*, 2012). The NE monsoon is also referred to as the 'retreating monsoon' (Rajeevan *et al.*, 2012) and the SW monsoon may be considered as dominant (Maury, 2003). The onset of the SW monsoon is sudden, extremely variable and has complex teleconnections with many global climate processes which are also influenced by local phenomena (Pradhan *et al.*, 2017). The retreat of the SW monsoon is reported to show opposite trends with these processes. However, it is more gradual (Walker and Bordoni, 2016) and it is affected by factors such as the thermodynamic behaviour of the monsoon (Raju and Bhatla, 2014).

The contrast between the onset and retreat of the SW monsoon means different methods are required to predict the events. For example, means of capturing the onset of the SW monsoon include the use of the monsoon index which has been shown to be accurate (Fasullo and Webster, 2003) but cannot predict its retreat (Wang *et al.,* 2009). Similarly, principal component regression models have been used to accurately predict the onset of the SW monsoon using parameters established from convective, thermal and circulation patterns (Wang *et al.*, 2009) but they are not used to predict retreat (Wang *et al.*, 2009).

The prediction models in the current study followed a similar pattern whereby the model that can most accurately predict the manta proportions during the onset of the SW monsoon (March and April) has the least predictive power during its retreat

(December) and visa verse (Table 5 and 6). April and March were not accurately predicted by any of the models which highlight that this may be the time when the SW monsoon is most variable.

In the Maldives fishing-related mortality has been alleviated by fishing bans (Sinan *et al.,* 2011), so a critical influence on manta ray survival is carrying capacity (Ward-Paige *et al.*, 2013) under bottom-up control which depends predominantly on zooplankton (Jaine *et al.*, 2012). Zooplankton relies on primary productivity (Cury *et al.*, 2015) which is dependent on wind activity (Deik *et al.*, 2017)**.**

Evidence of the historical influence (8-10 Ma) of climate change on the South Asian Monsoon (SAM) has been presented in a study that showed that the development of stronger winds enhanced primary productivity in the Indian Ocean (Gupta *et al.*, 2004). The modern SAM is now under the influence of anthropogenic climate change (Carmichael *et al.*, 2009; Turner and Annamalai, 2012) for example, increasing industrialisation has increased emissions of aerosols (Turner and Annamalai, 2012) which absorb and scatter thermal radiation (Mishra *et al.*, 2015). Aerosol burden over India is reported to be approximately three times higher than the global mean values (Pandey *et al.*, 2017). Using observations and climate model experiments Roxy *et al.* (2015) provide evidence that these emissions have subdued warming over this crucial land masses and surface temperatures are following a cooling trend (Roxy *et al.*, 2015). Along with the warming of the Indian Ocean through meridional oceanic heat transport (Turner and Annamalai, 2012), this cooling has reduced the land-sea thermal gradient (Roxy *et al.*, 2015). This reduced thermal contrast effects the seasonal migration of the ITCZ, the shift of which is an essential component in the onset and retreat of the SW monsoon (Yadav, 2013). Meteorological teleconnections to the SW monsoon and their possible effects have been highlighted in various studies (Joseph and Simon, 2005; Kalapureddy *et al.*, 2007; Sanil Kumar and George, 2016). For example, two synoptic-scale jets that have been identified as influencing the strength of the SW monsoon are the Low-Level Jet (LLJ) and Tropical Easterly Jet (TEJ) (Kalapureddy *et al.*, 2007). A study by Joseph and Simon (2005) report that the LLJ has been following a weakening trend since the 1950s linked to changes in atmospheric heat balance. This tread showed 'weak' spells in the SW monsoon increasing by 30% (Joseph and Simon, 2005) where the magnitude of the wind is reduced (Sanil Kumar and George, 2016). Similarly, Abish *et al.* (2013) observed the

same trend in the TEJ and attributed it to cooling of land masses and warming of the Indian Ocean (Abish *et al.*, 2013).

Extreme variabilities in onset and strength of the SW monsoon could be deleterious to manta rays. As a K-selected species, their life history is characterised by low fecundity (Kitchen-Wheeler, Ari and Edwards, 2012) slow growth and late maturation (Ward-Paige *et al.*, 2013). As fecundity is linked to food availability, changes in the monsoon that influence primary productivity may be detrimental to the long-term survival of manta ray populations in the Maldives (Stevens, 2016). The SW monsoon is the stronger of the two monsoons (Maury, 2003) which is when peaks in primary productivity occur (Deik *et al.*, 2017) making it an essential time for the manta rays particularly for reproduction (Stevens, 2016).

Furthermore, manta rays are an ovoviviparous species which is an energetically expensive mode of reproduction (Marshall and Bennett, 2010). Between pregnancies, females require sufficient food sources need to increase lipid stores to provide enough energy to breed again (Carrier *et al.*, 2004). These recuperation periods are long thus reproductive cycles are thought to be biennial, triennial (Marshall and Bennett, 2010) or even less frequent with evidence that a manta ray may only produce a few pups during their lifetime (Stevens, 2016). Potentially, even small dips in food resources will negatively affect fecundity and offspring survivorship (Stevens, 2016).

Primary productivity has been linked to the body size of planktivores (Pyenson and Vermeij, 2016). Body size can also affect reproductive success, for example, Deakos (2012) investigated the reproductive ecology of reef manta rays in Maui, Hawaii and reported that larger females had greater mating success and were able to reproduce more often (Deakos, 2012).

Evidence supports the importance of the SW monsoon and its influence over WMAN and EMAN during both the NE and SW monsoon months. However, yet to be identified are factors that are inducing manta ray migration which occurs during the transition months. Migrations may occur in response to changes in environmental conditions (Graham, 2003) for instance, the predictions of EMAN and WMAN during the retreat of the SW monsoon (November and December) vary between accurate and just above the acceptable margin (Table 4 and Table 5) which may indicate that the SW monsoon winds may be an influence. One interpretation may be that as the SW monsoon winds

decline, the ocean surface currents become weaker which may be a cue to migrate. The inaccurate predictions during the onset of the SW monsoon in March and April suggest that something other than these variables maybe triggering migration. Most notably, this is supported by the EMAN prediction result in April 2017 using the monthly percentage of days the wind direction represents the SW monsoon (WDSW) (Table 5). During this month, WDSW was 100% therefore 94.5% EMAN was predicted however, the actual EMAN was only 27.6%.

Manta rays have multiple sensory channels that may be utilised for migration these include olfactory, visual and lateral line systems (Deakos, 2010). Olfactory has been shown to play a part in homing and navigation in other elasmobranch species (Edrén and Gruber, 2005) where biochemical products released by organisms is used to detect prey (Deakos, 2010). Olfaction is one of the most important senses for elasmobranch because chemical signals may be detected in the marine environment over much larger distances than other sensory signals (Meredith and Kajiura, 2010). Ari and Correia (2008) conducted a behavioural study on a captive manta ray (*Manta birostris*) to assist in identifying possible environmental cues associated with feeding behaviour. They concluded that searching for food appeared to be triggered, in part, by olfactory stimuli. Ari and Correia (2008) also suggest that cognitive ability plays a role, as the manta displayed behaviour that indicated it associated a specific location with food. Evidence presented also indicated that the manta ray made use of its internal biological clock to predict when food was going to be available (Ari and Correia, 2008).

Although this study was limited to a single manta ray in captivity, the implications of the results should be considered as they suggest that mantas may learn where and when to find food (Ari and Correia, 2008). In the Maldives, locations that currently provide seasonal feeding opportunities may be impacted by climate change (Deik *et al.,* 2017). In particular, the weakening of the SW monsoon could lead to reduced upwelling thus reducing food availability (Deik *et al.*, 2017). Under these conditions, if the times that mantas frequent the east and the west side of the atolls based on an internal biological clock and long-term spatial memory (Deakos, 2010) sudden changes could mean manta rays are unable to find food, therefore, reducing survivorship.

Conclusion

Successful conservation of *Manta alfredi* in the Maldives can only be continued if efforts are prioritised relative to the impacts of the threats to the species (Zydelis *et al.*, 2009). MLR modelling and prediction analysis in this study has helped to develop the current understanding of the relationships between manta ray distribution in the Maldives and environmental variables linked to the monsoon. The models used to estimate the monthly proportion of manta rays on the east and the west side of the atolls is a useful tool that may help focus conservation efforts as manta ray presence may be predicted using the SW monsoon winds. However, further model development is required to predict migration to help establish the timing more accurately.

The SW monsoon winds are essential for primary productivity and therefore zooplankton biomass (Elliott *et al.*, 2012). Any changes in the SW monsoon winds may have a drastic impact on prey resources for the manta rays thus are a critical component of their long-term survival (Stevens, 2016). The results of this study have provided a baseline for further research which is required to assess how manta ray conservation in the Maldives may be affected by the reported weakening of the SW monsoon.

Future research should involve modelling of the manta ray's distribution during the onset and the retreat of the SW monsoon independently so to assist in identifying migration cues. Further environmental parameters should be considered along with those of in this study such as ocean surface currents and sea surface temperatures. *In situ* zooplankton composition data should be included as this is expected to be an essential influence of manta ray migration. However, as there will be gaps in historical zooplankton data, efforts should also be made to efficiently quantify Chl-a concentrations at the locations where manta rays are present.

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Conflicts of Interest

The author declares no conflict of interest.

References

Abdi, H. (2003) 'Partial regression coefficients', in *Encyclopedia of Social Sciences Research Methods*. Thousand Oaks (CA): SAGE, pp. 1–4.

Abish, B., Joseph, P. V. and Johannessen, O. M. (2013) 'Weakening trend of the tropical easterly jet stream of the boreal summer monsoon season 1950-2009', *Journal of Climate*, 26(23), pp. 9408–9414.

Anderson, R. C., Adam, M. S. and Goes, J. I. (2011a) 'From monsoons to mantas: Seasonal distribution of Manta alfredi in the Maldives', *Fisheries Oceanography*, 20(2), pp. 104–113.

Anderson, R. C., Adam, M. S., Kitchen-Wheeler, A.-M. and Stevens, G. (2011b) 'Extent and Economic Value of Manta Ray Watching in Maldives', *Tourism in Marine Environments*, 7(1), pp. 15–27.

Anderson, R. C., Branch, T. A., Alagiyawadu, A., Baldwin, R. and Marsac, F. (2012) 'Seasonal distribution , movements and taxonomic status of blue whales (Balaenoptera musculus) in the northern Indian Ocean', *Journal of Cetacean Research and Management*, 12(2), pp. 203–218.

Ari, C. and Correia, J. P. (2008) 'Role of sensory cues on food searching behavior of a captive Manta birostris (Chondrichtyes, Mobulidae)', *Zoo Biology*, 27(4), pp. 294–304.

Armstrong, A. O., Armstrong, A. J., Jaine, F. R. A., Couturier, L. I. E., Fiora, K., Uribe-Palomino, J., Weeks, S. J., Townsend, K. A., Bennett, M. B. and Richardson, A. J. (2016) 'Prey Density Threshold and Tidal Influence on Reef Manta Ray Foraging at an Aggregation Site on the Great Barrier Reef', *PloS one*, 11(5). e0153393.

Arnold, T. W. (2010) 'Uninformative Parameters and Model Selection Using Akaike's Information Criterion', *Journal of Wildlife Management*, 74(6), pp. 1175–1178.

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

Beaujean, A. A. (2014) 'Sample size determination for regression models using

Monte Carlo methods in R', *Practical Assessment, Research & Evaluation*, 19(12), pp. 1–16.

Betzler, C., Eberli, G. P., Kroon, D., Wright, J. D., Swart, P. K., Nath, B. N., Alvarez-Zarikian, C. A., Alonso-García, M., Bialik, O. M., Blättler, C. L., Guo, J. A., Haffen, S., Horozal, S., Inoue, M., Jovane, L., Lanci, L., Laya, J. C., Mee, A. L. H., Lüdmann, T., Nakakuni, M., Niino, K., Petruny, L. M., Pratiwi, S. D., Reijmer, J. J. G., Reolid, J., Slagle, A. L., Sloss, C. R., Su, X., Yao, Z. and Young, J. R. (2016) 'The abrupt onset of the modern South Asian Monsoon winds', *Scientific Reports*, 6(1), p. 1-10.

Bollasina, M. A., Ming, Y. and Ramaswamy, V. (2011) 'Anthropogenic aerosols and the weakening of the south asian summer monsoon', *Science*, 334(6055), pp. 502–505.

Brian, A., Venables, B., Bates, D. M., Firth, D. and Ripley, M. B. (2018) 'Package " MASS "'. Available at: https://cran.r-project.org/web/packages/MASS/MASS.pdf. (Accessed: 12 January 2018)

Brown, K. T., Bender-Champ, D., Bryant, D. E. P., Dove, S. and Hoegh-Guldberg, O. (2017) 'Human activities influence benthic community structure and the composition of the coral-algal interactions in the central Maldives', *Journal of Experimental Marine Biology and Ecology*. Elsevier, 497(March), pp. 33–40.

Bruce, J. G., Johnson, D. R. and Kindle, J. C. (1994) 'Evidence for eddy formation in the eastern Arabian Sea during the northeast monsoon', *Journal of Geophysical Research*, 99(C4), pp. 7651–7664.

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

Carmichael, G. R., Adhikary, B., Kulkarni, S., D'Allura, A., Tang, Y., Streets, D., Zhang, Q., Bond, T. C., Ramanathan, V., Jamroensan, A. and Marrapu, P. (2009) 'Asian aerosols: Current and year 2030 distributions and implications to human health and regional climate change', *Environmental Science and Technology*, 43(15), pp. 5811–5817.

Carrier, J. C., Pratt, H. L. and Castro, J. I. (2004) 'Biology of Sharks and Their

Relatives', in '*Biology of Sharks and Their Relatives'*. Boca Raton, FL: CRC Press, pp. 269–286.

Charlotte, B. V, Simon, E. K., George, G., Yesodharan, S. and Ruchith, R. D. (2012) 'Intra-seasonal oscillation of north east monsoon over southern peninsular India-an investigation', *International Journal of Scientific and Research Publications*, 2(8), pp. 1–22.

Crawley, M. J. (2013) *The R Book.* 2nd edn. West Sussex: John Wiley & Sons Inc.

Cury, P., Shannon, L. and Shin, Y. (2015) 'The functioning of marine ecosystems: a fisheries perspective.', in *Responsible fisheries in the marine ecosystem*, pp. 103–123.

Deakos, M. H. (2010) 'Ecology and social behavior of a resident manta ray (Manta alfredi) population off Maui, Hawaii', PhD Thesis, University of Hawaiʻi.

Deakos, M. H. (2012) 'The reproductive ecology of resident manta rays (Manta alfredi) off Maui, Hawaii, with an emphasis on body size', *Environmental Biology of Fishes*, 94(2), pp. 443–456.

Deakos, M. H., Baker, J. D. and Bejder, L. (2011) 'Characteristics of a manta ray Manta alfredi population off Maui, Hawaii, and implications for management', *Marine Ecology Progress Series*, 429, pp. 245–260.

Deik, H., Reuning, L. and Pfeiffer, M. (2017) 'Orbital scale variation of primary productivity in the central equatorial Indian Ocean (Maldives) during the early Pliocene', *Palaeogeography, Palaeoclimatology, Palaeoecology*. Elsevier B.V., 480, pp. 33–41.

Edrén, S. M. C. and Gruber, S. H. (2005) 'Homing ability of young lemon sharks, Negaprion brevirostris', *Environmental Biology of Fishes*, 72(3), pp. 267–281.

Elliott, J., Patterson, M. and Gleiber, M. (2012) 'Detecting " Island Mass Effect " through remote sensing', *Proceedings of the 12th International Coral Reef Symposium*, (July), pp. 9–13.

Fasullo, J. and Webster, P. J. (2003) 'A hydrological definition of Indian Monsoon onset and withdrawal', *Journal of Climate*, 16(19), pp. 3200–3211.

Field, A., Miles, J. and Field, Z. (2012) *Discovering Statistics Using R.* London: SAGE.

Goldbogen, J. A., Hazen, E. L., Friedlaender, A. S., Calambokidis, J., DeRuiter, S. L., Stimpert, A. K. and Southall, B. L. (2015) 'Prey density and distribution drive the three-dimensional foraging strategies of the largest filter feeder', *Functional Ecology*, 29(7), pp. 951–961.

Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., Merrifield, M. A., Friedlander, A. M., Ehses, J. S., Young, C. W., Dillon, A. K. and Williams, G. J. (2016) 'Near-island biological hotspots in barren ocean basins', *Nature Communications*. Nature Publishing Group, 7, pp. 1–8.

Graham, R. T. (2003) 'Behaviour and conservation of whale sharks on the Belize Barrier Reef, Environment Department'. PhD Thesis. University of York.

Grueber, C. E., Nakagawa, S., Laws, R. J. and Jamieson, I. G. (2011) 'Multimodel inference in ecology and evolution: Challenges and solutions', *Journal of Evolutionary Biology*, 24(4), pp. 699–711.

Gupta, A. K., Singh, R. K., Joseph, S. and Thomas, E. (2004) 'Indian Ocean high-productivity event (10-8 Ma): Linked to global cooling or to the initiation of the Indian monsoons?', *Geology*, 32(9), pp. 753–756.

Hamra, G. B., Kaufman, J. S. and Vahratian, A. (2015) 'Model averaging for improving inference from causal diagrams', *International Journal of Environmental Research and Public Health*, 12(8), pp. 9391–9407.

Hurvich, C. M. and Tsai, C. L. (1991) 'Bias of the corrected aic criterion for underfitted regression and time series models', *Biometrika*, 78(3), pp. 499–509.

Jaine, F. R. A., Couturier, L. I. E., Weeks, S. J., Townsend, Kathy A. Bennett, M. B., Fiora, K. and Richardson, A. J. (2012) 'When Giants Turn Up: Sighting Trends, Environmental Influences and Habitat Use of the Manta Ray Manta alfredi at a Coral Reef', *PLoS ONE*, 7(10). e46170.

Joseph, P. V. and Simon, A. (2005) 'Weakening trend of the southwest monsoon current through peninsular India from 1950 to the present', *Current Science*, 89(4), pp. 687–694.

Kalapureddy, M. C. R., Rao, D. N., Jain, A. R. and Ohno, Y. (2007) 'Wind profiler observations of a monsoon low-level jet over a tropical Indian station', *Annales Geophysicae*, 25(10), pp. 2125–2137.

Kamil Bartoń (2018) 'Package " MuMIn "'. Available at: https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf. (Accessed: 12 January 2018)

Kitchen-Wheeler, a-M. (2010) 'Visual identification of individual manta ray (Manta alfredi) in the Maldives Islands, Western Indian Ocean', *Marine Biology Research*. Taylor & Francis, 6(4), pp. 351–363.

Kitchen-Wheeler, A. M., Ari, C. and Edwards, A. J. (2012) 'Population estimates of Alfred mantas (Manta alfredi) in central Maldives atolls: North Male, Ari and Baa', *Environmental Biology of Fishes*, 93(4), pp. 557–575.

Kuiter, R. H. and Godfrey, T. (2014) *Fishes of the Maldives – Indian Ocean*. Male: Atoll Editions.

Livingston, R. J. (2005) *Restoration of Aquatic Systems*. London: Taylor & Francis Inc.

Lumley, T. (2017) 'Package " leaps "'. Available at: https://cran.r-project.org/web/packages/leaps/leaps.pdf. (Accessed: 18 January 2018)

Marshall, A. D. and Bennett, M. B. (2010) 'Reproductive ecology of the reef manta ray Manta alfredi in southern Mozambique', *Journal of Fish Biology*, 77(1), pp. 169–190.

Marshall, A., Kashiwagi, T., Bennett, M. B., Deakos, M., Stevens, G., McGregor, F., Clark, T., Ishihara, H. and Sato, K. (2011) *Reef Manta Ray (Manta alfredi)*, *The IUCN Red List of Threatened Species 2016*.

Maury, M. F. (2003) *The Physical Geography of the Sea and Its Meteorology*. New York: Dover Publications Inc.

Meredith, T. L. and Kajiura, S. M. (2010) 'Olfactory morphology and physiology of elasmobranchs.', *The Journal of experimental biology*, 213(Pt 20), pp. 3449–3456.

Millo, G. and Mitchell, D. (2017) 'Package "lmtest"'. Available at: https://cran.r-project.org/web/packages/lmtest/lmtest.pdf. (Accessed: 3 February 2018)

Mishra, A. K., Koren, I. and Rudich, Y. (2015) 'Effect of aerosol vertical distribution on aerosol-radiation interaction: A theoretical prospect', *Heliyon*. Elsevier Ltd, 1(2).

Moses, W. J., Gitelson, A. A., Berdnikov, S. and Povazhnyy, V. (2009) 'Estimation of chlorophyll- *a* concentration in case II waters using MODIS and MERIS data— successes and challenges', *Environmental Research Letters*, 4(4), p. 1-8.

Oguri, M. S., Doty, M. (1956) 'The Island Mass Effect', *ICES Journal of Marine Science*, 1(March), pp. 33–37.

Pandey, S. K., Vinoj, V., Landu, K. and Babu, S. S. (2017) 'Declining pre-monsoon dust loading over South Asia: Signature of a changing regional climate', *Scientific Reports*. Springer US, 7(1), pp. 1–10.

Pena, E. and Slate, E. (2006) 'Package 'gvlma''. Available at: https://cran.r-project.org/web/packages/gvlma/gvlma.pdf. (Accessed: 3 February 2018).

Pradhan, M., Rao, A. S., Srivastava, A., Dakate, A., Salunke, K. and Shameera, K. S. (2017) 'Prediction of Indian Summer-Monsoon Onset Variability: A Season in Advance', *Scientific Reports*. Springer US, 7(1), pp. 1–14.

Putra, M., Lewis, S., Kurniasih, E., Prabuning, D. and Faiqoh, E. (2016) 'Plankton Biomass Models Based on GIS and Remote Sensing Technique for Predicting Marine Megafauna Hotspots in the Solor Waters', *IOP Conference Series: Earth and Environmental Science*, 47, p. 1-19.

Pyenson, N. D. and Vermeij, G. J. (2016) 'The rise of ocean giants: maximum body size in Cenozoic marine mammals as an indicator for productivity in the Pacific and Atlantic Oceans', *Biology Letters*, 12(7), p. 1-4.

R Core Team (2013) *R:* A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. Available at: http://www.r-project.org/ (Accessed: 30 October 2017).

Rajeevan, M., Unnikrishnan, C. K., Bhate, J., Niranjan Kumar, K. and Sreekala, P. P. (2012) 'Northeast monsoon over India: Variability and prediction', *Meteorological Applications*, 19(2), pp. 226–236.

Raju, P. V. S. and Bhatla, R. (2014) 'Evolution of withdrawal features of the southwest monsoon over India', *International Journal of Climatology*, 34(6), pp.

1860–1872.

Rohner, C. A., Pierce, S. J., Marshall, A. D., Weeks, S. J., Bennett, M. B. and 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, pp. 153–168.

Roxy, M. K., Ritika, K., Terray, P., Murtugudde, R., Ashok, K. and Goswami, B. N. (2015) 'Drying of Indian subcontinent by rapid Indian ocean warming and a weakening land-sea thermal gradient', *Nature Communications*. Nature Publishing Group, 6(May), pp. 1–10.

Sanil Kumar, V. and George, J. (2016) 'Influence of Indian summer monsoon variability on the surface waves in the coastal regions of eastern Arabian Sea', *Annales Geophysicae*, 34(10), pp. 871–885.

Sasamal, S. K. (2006) 'Island mass effect around the Maldives during the winter months of 2003 and 2004', *International Journal of Remote Sensing*, 27(22), pp. 5087–5093.

Schott, F. A. and McCreary, J. P. (2001) 'The monsoon circulation of the Indian Ocean', *Progress in Oceanography*, 51(1), pp. 1–123.

Sequeira, A. M. M., Mellin, C., Fordham, D. A., Meekan, M. G. and Bradshaw, C. J. A. (2014) 'Predicting current and future global distributions of whale sharks', *Global Change Biology*, 20(3), pp. 778–789.

Sinan, H., Adam, M. S. and Anderson, R. C. (2011) *Status of Shark Fisheries in the Maldives*. Malé. Available at: http://www.iotc.org/documents/status-shark-fisheries-maldives. (Accessed: 12 February 2018).

Stevens, G. M. W. (2016) 'Conservation and Population Ecology of Manta Rays in the Maldives'. PhD Thesis. University of York.

Sun, Y. and Ding, Y. H. (2011) 'Responses of South and East Asian summer monsoons to different land-sea temperature increases under a warming scenario', *Chinese Science Bulletin*, 56(25), pp. 2718–2726.

Symonds, M. R. E. and Moussalli, A. (2011) 'A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's

information criterion', *Behavioral Ecology and Sociobiology*, 65(1), pp. 13–21.

Turner, A. G. and Annamalai, H. (2012) 'Climate change and the South Asian summer monsoon', *Nature Climate Change*. Nature Publishing Group, 2(8), pp. 587–595.

Walker, J. M. and Bordoni, S. (2016) 'Onset and withdrawal of the large-scale South Asian monsoon: A dynamical definition using change point detection', *Geophysical Research Letters*, 43(22), p. 11,815-11,822.

Wang, B., Ding, Q. and Joseph, P. V. (2009) 'Objective definition of the Indian summer monsoon onset', *Journal of Climate*, 22(12), pp. 3303–3316.

Ward-Paige, C. A., Davis, B. and Worm, B. (2013) 'Global population trends and human use patterns of Manta and Mobula rays', *PLoS ONE*, 8(9). e74835.

Weeks, S. J., Magno-Canto, M. M., Jaine, F. R. A., Brodie, J. and Richardson, A. J. (2015) 'Unique sequence of events triggers manta ray feeding frenzy in the Southern Great Barrier Reef, Australia', *Remote Sensing*, 7(3), pp. 3138–3152.

Yadav, R. K. (2013) 'Emerging role of Indian ocean on Indian northeast monsoon', *Climate Dynamics*, 41(1), pp. 105–116.

Zydelis, R., Wallace, B. P., Gilman, E. L. and Werner, T. B. (2009) 'Conservation of marine megafauna through minimization of fisheries bycatch', *Conservation Biology*, 23(3), pp. 608–616.