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Environmental, spatial and temporal effects on the number and behaviour of manta rays in Baa atoll, Maldives

Saphire Indianna Emily Cartlidge supervised by Dr Kathryn Arnold

Disclaimer

Acknowledgements

I would like to thank Dr Kathryn Arnold for all her help supervising me with this project. I would also like to thank the Manta Trust for the use of their data and both Guy Stevens and Annie Murray for their assistance with the dataset.

Abstract

Manta rays are known to aggregate at particular sites in larger number than at other sites and are also known to exhibit different behaviours at different sites. Their numbers and behaviours are influenced by environmental variables and vary on both a spatial and temporal scale. This study used generalised linear models to determine which variables were influencing the number and behaviour of manta rays in Baa atoll, Maldives at 8 study sites. The variables were year, month, site, number of manta rays sighted, behaviour, chlorophyll a concentration, sea surface temperature, wind direction and speed. The results indicated that the number and behaviour of the manta rays varied between year, month and site and that the location of the site with regard to currents is key to differences seen in aggregation size and behaviour. Significantly fewer manta rays were seen in sea surface temperatures above 29.75^{o}C, concurring with other studies that manta rays may have an upper thermal limit of 30^{o}C. Additionally fewer manta rays were seen in weeks where the chlorophyll concentrations were lower, which could potentially be due to the blooms of phytoplankton having already been eaten by zooplankton. The presence of courtship behaviour could not be linked to any of the variables in this study which is likely due to limitations in the data.

Introduction

The spatial and temporal patterns of marine organisms are affected by biotic and abiotic environmental factors and as humans are putting increasing pressure on the oceans it is vital to understand the relationship between a species and the environmental factors that influence its behaviour (Sims, 2003; Snickars *et al.*, 2014). Of these environmental factors both the availability of food and sea surface temperature (SST) are important in determining the patterns of marine organisms.

Food availability is a strong driving factor in the growth of sessile organisms such as the mussel *Mytilus edulis* (Page & Hubbard, 1987) as well as the movements of marine predators that actively search for their prey (Sims *et al*,. 2008). It particularly affects the spatial patterns of filter feeders such as many species of elasmobranch and cetacean that are the top of a short food chain (phytoplankton-zooplankton-megaplanktivore). As zooplankton makes up a considerable proportion of a filter feeders diet it is crucial for them to find foraging areas that have high enough aggregations of zooplankton to support them (Sims et al., 2005). Spatial patterns with relation to food availability have been studied on multiple species such as the basking shark, *Cetorhinus maximus*, which actively searches for areas of high productivity to forage in (Sims, 2003). Additionally Whale sharks, *Rhincodon typus*, are known to predictably be found in specific coastal regions to exploit short lived seasonally high abundances of zooplankton (Sleeman et al., 2010). In Monterey Bay, California, Blue Whales, *Balaenoptera musculus* were found to seasonally migrate with relation to increased productivity caused by upwellings (Croll *et al*., 2005). Upwellings bring dissolved CO_2, macronutrients and micronutrients to the surface which is vital to the growth of phytoplankton (Behrenfeld *et al*., 2006). The increased growth in phytoplankton caused dense aggregations of euphausiids (prey) in the foraging areas of Blue Whales.

Sea temperature can play an important role in the distribution of species limited by temperature range (Perry *et al.,* 2005). Cartamil *et al.* (2016) studied the movements of juvenile common thresher sharks and found them to be predominantly in only a 3^oC

temperature range and to spend time at night in significantly warmer waters than during the day. Therefore sea surface temperature has become of particular importance to study in relation to consequences of climate change (Pörtner, 2002). Sea surface temperature can also directly influence the level of primary productivity and studies show bottom up processes (resources limit the abundance of predators) to control many marine ecosystems, particularly high diversity ecosystems in warm waters (Gremillet *et al.*, 2008; Frank *et al*., 2007). In the East Bering Sea, sea surface temperature was found to correlate with the abundance of Humpback whales, *Megaptera novaeangliae,* as did chlorophyll a concentration and euphausiid biomass (Zerbini *et al.*, 2016). High SSTs can cause a nutricline as the nutrient rich deeper, cooler water cannot mix with the warm surface waters where the phytoplankton are (Yang *et al*., 2017). Therefore it is important to study the effects of temperature on marine organisms separately as well as in conjunction with primary productivity.

Manta rays are planktivorous elasmobranchs separated into two species, *Manta birostris* commonly known as the oceanic manta which is distinctive from *Manta alfredi*, the reef manta, by certain external characteristics described by Marshall *et al.* (2009). Manta rays have a wide ranged distribution in tropical and subtropical waters, including the Maldives where they occur in large numbers (Kitchen-Wheeler, 2010; Anderson *et al.,* 2011). In fact, in a study by Kitchen-Wheeler *et al*. in 2012, where *Manta alfredi* in the Maldives were individually identified, they recorded the largest population in the world. Manta rays in the Maldives are known to seasonally migrate, influenced by the currents caused by the monsoon winds which change direction biannually (Anderson *et al.,* 2011). May to October is the southwest monsoon which causes currents to flow generally to the east. December to

March is the northeast monsoon which causes currents to flow mainly to the west (Shankar *et al.*, 2002). On the downstream side of the atolls, waters rich in nutrients are brought to the surface by the movement of the currents over the Maldives ridge, allowing blooms of phytoplankton which supports an explosion of zooplankton. As the diet of manta rays is almost entirely composed of zooplankton they are attracted to these high concentrations (Anderson *et al.,* 2011). The movements of manta rays have also been studied in Komodo National Park, Indonesia where some manta rays had high site fidelity, returning to the same site almost every day for up to three months (Dewar *et al.*, 2008). However, the majority of manta rays visited at least two areas and there were long periods were some of the tagged mantas were not recorded by any of the receivers in the park. This raises the question of what causes the manta rays to have a high site fidelity but also what causes them to move onto different sites or out of the area altogether. From a conservation perspective, it is important to understand what influences the number and behaviour of manta rays in order to be able to give protection to sites which have the best conditions for large numbers of manta rays to flourish. A key area of manta ray conservation to study is the reproductive cycle. Elasmobranchs in coastal tropical waters are known to move to areas where the water temperature is warm and stable (Conrath & Musick, 2012).

The aims of this study were to determine the environmental, spatial and temporal effects of on the number and behaviour of manta rays in Baa atoll in the Maldives. This was broken down into the effects on the environmental variables, the effects on the number of manta rays seen per 15 minutes, the effects on behaviour and were there any differences between the variables when courtship was observed?

Methods

Site description

8 sites where manta rays were known to aggregate in Baa atoll were included in this study. Baa atoll is on the western side of the double chain atolls in the Northern Province of the Maldives. It is 38km wide and 42km long and contains 75 reefs (Jimenez *et al.*, 2012). The 8 sites were Hanifaru Bay, Reethi Beach, Veyofushi, Hurai Faru, Hanifaru Beyru, Dharavandhoo Corner, Dhigu Thila and Dharavandhoo Thila (Figure 1). All the sites are on the east side of the atoll which in the South West monsoon is the downstream side, meaning high numbers of manta rays and a higher chance of seeing manta rays was to be expected in these locations during the South West monsoon (Anderson *et al.*, 2011).

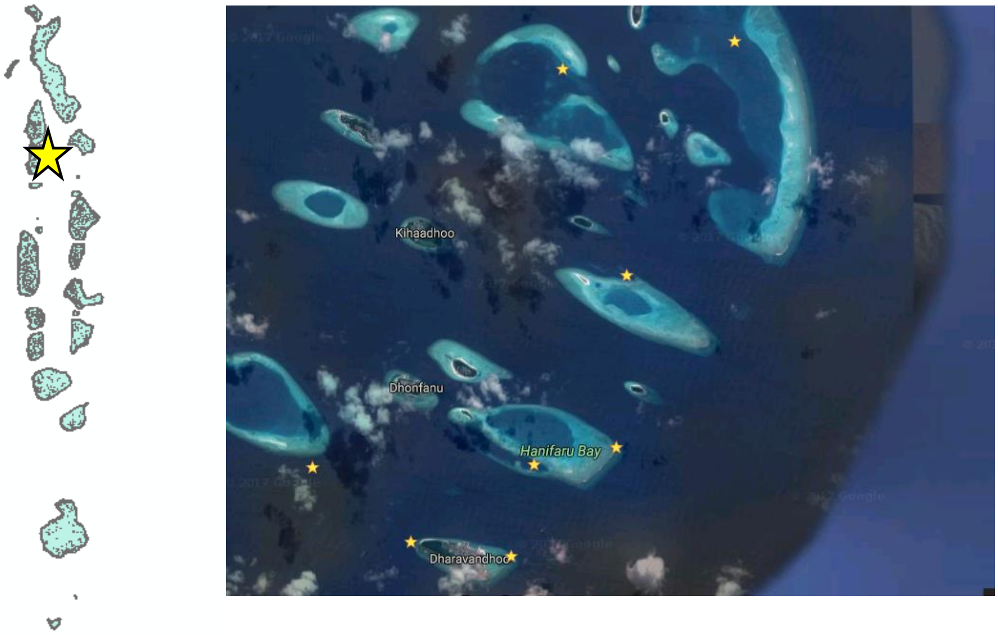

Figure 1. Map showing the location of Baa atoll in the Maldives (Revolutionary GIS, 2014) and a zoomed in map of Baa atoll showing the location of the 8 study sites (Google Maps, 2017).

Environmental data

The SST (^{o}C) and chlorophyll a (milligrams per cubic metre) data used was from the Environmental Research Division's Data Access Program (ERDDAP) by the National Oceanic and Atmospheric Administration (NOAA) (NOAA, 2017). There were too many days where no data was recorded for chlorophyll a due to cloud cover, therefore weekly averages provided better data cover. For chlorophyll a, data from either NASA Visible and Infrared Imager/Radiometer Suite (VIIRS) or Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua was used as sometimes one or the other did not have data coverage for a specific site, both have a resolution to 5km. For the SST, the data was also weekly averages from Geostationary Operational Environmental Satellite – Polar Orbiting Environmental Satellite (GOES-POES) which has a resolution to 5km.

Manta Trust data

The manta data which included the number of manta rays seen at each site, the time spent at that site, the behaviour of the manta rays including whether courtship was observed, the wind speed and direction used in this study was collected by The Manta Trust. The years studied were 2012, 2013 and 2014 as these were the most recent years with a completed data set from the Manta Trust. Sighting surveys were done from May to November which is the South West monsoon when currents flow predominantly to the east (Shankar *et al.*, 2002).

The dataset

The number of manta rays seen each week at each site were totalled as well as the time spent at each site that week. To control for effort, the number of manta rays seen per 15 minutes was calculated as for some weeks at some sites only 15 minutes were spent there in total. The dominant behaviour observed at each site during that week was noted as either feeding, cleaning, cruising or N/A if no manta rays were seen and whether courtship was observed or not. The average wind speed and direction were calculated for each week and the weekly average SST and chlorophyll were taken for each site from ERDDAP using co-ordinates supplied by the Manta Trust for sites. Therefore the variables analysed were year (2012, 2013 and 2014), month (May to November), site, control (number of manta rays seen per 15 minutes), behaviour, courtship (presence/absence), SST (^{o}C), chlorophyll a (milligrams per cubic metre), wind speed (mph) and wind direction (^{o}).

Data analyses

Statistical analyses of these variables were carried out using R (version 3.0.2; http://cran.r-project.org). Initially each variable was plotted to check for skew and if necessary transformed to deal with any strong skew as follows; control (double log) and chlorophyll (triple square root). In order to decrease the intercorrelation between the predictor variables Pearson correlation was used to create sets of variables with Variance Inflation Factor (VIF) scores <2 for each model (Zuur, Leno & Elphick 2010). The models were checked for over dispersion by dividing the residual deviance by the degrees of freedom and any results >1.5 would have been considered to be over dispersed however none of the models in this study were over dispersed (Crawley 2005).

The environmental variables; chlorophyll, SST, wind speed and direction were modelled as response variables in Generalised Linear Models (GLMs) against year, month, site and each other to see what they were significantly correlated with. Then GLMs with the response variables of control, behaviour and courtship were run and following the results of the environmental GLMs, 3 GLMs for each response variable were run with the predictor variables split up so that no GLM contained variables that had significant results in the environmental GLMs. To every p value calculated by the models for each variable, False Discovery Rate was applied (FDR) (Benjamini & Hochberg 1995) to create a 95% significance alpha cut-off value. Additionally where more than one behaviour was observed between weeks at the same site, the chlorophyll at each site when the different behaviours occurred was analysed. As the test was looking for a significant difference between two sets of data, if the both the sets of data were normally distributed then a t-test was used however if the data were not normally distributed a Kruskall-Wallis test was used.

Results

Environmental variables

The concentration of chlorophyll was negatively correlated with SST, with high concentrations found at low SST (Table 1a; Figure 2). SST varied significantly between months with temperatures considerably higher in May, dropping in June and rising slightly in August when the wind speed dropped (Table 1b; Figure 3) as SSTs were generally higher in low wind speeds (Table 1b; Figure 4). Wind direction varied significantly between months (Table 1c), being westerly in May and June and gradually becoming more north westerly until September and staying west north west in October and November. Wind speed varied significantly between months and years, on average it was highest in June and lowest in November (Figure 5) which coincides with the drop in SST in June. Wind speed was lowest in 2012 and highest in 2014 (Table 1d).

Table 1. GLMs of the environmental variables against their predictor variables. Model D= deviance explained by the model, E=estimate, D= deviance explained by that variable. Bold type = significant variables following FDR correction.

Model	Model statistics
a) Chlorophyll compared to the variables; year, month, site, SST, wind direction and wind speed Alpha=0.00833	AIC=-1009 Model D=15.520% Year: E=0.00557 D=0.5301% P=0.1487 Month: E=-0.00433 D=1.138% P=0.0343 Site: E=-0.000701 D=0.0569% P=0.6405 **SST: E=-0.0552 D=8.05% P=**$\mathbf{0.00344^{-5}}$ Wind direction: E=-0.000109 D=0.539% P=0.146 Wind speed: E=0.00182 D=0.6915% P=0.0996
b) SST compared to the variables; year, month, site, chlorophyll, wind direction and wind speed Alpha=0.025	AIC= 137.17 Model D=15.852% Year: E=-0.0140 D=0.115% P=0.499 **Month: E=-0.0418 D=3.807% P=0.000120** Site: E=-0.0135 D=0.714% P=0.0928 **Chlorophyll: E=-1.576 D=8.017% P=**$\mathbf{0.00344^{-5}}$ Wind direction: E=0.00612^{-2} D=0.00594% P=0.879 **Wind speed: E=-0.0216 D=3.503% P=0.000221**
c) Wind direction compared to the variables; year, month, site and wind speed Alpha=0.0125	AIC=3497.1 Model D=4.582% Year: E=-2.922 D= 0.310% P=0.296 **Month: E=5.257 D= 3.783% P=0.000281** Site: E=0.760 D=0.138% P=0.485 Wind speed: E=0.523 D=0.128% P=0.501
d) Wind speed compared to the variables; year, month, site, and wind direction Alpha=0.025	AIC=1678.6 Model D=30.062% **Year: E=0.623 D=2.167% P=0.00136** **Month: E=-1.008 D=28.344% P=**$\mathbf{0.002^{-13}}$ Site: E=0.00333 D=0% P=0.965 Wind direction: E=0.002567 D=0.0936% P=0.501

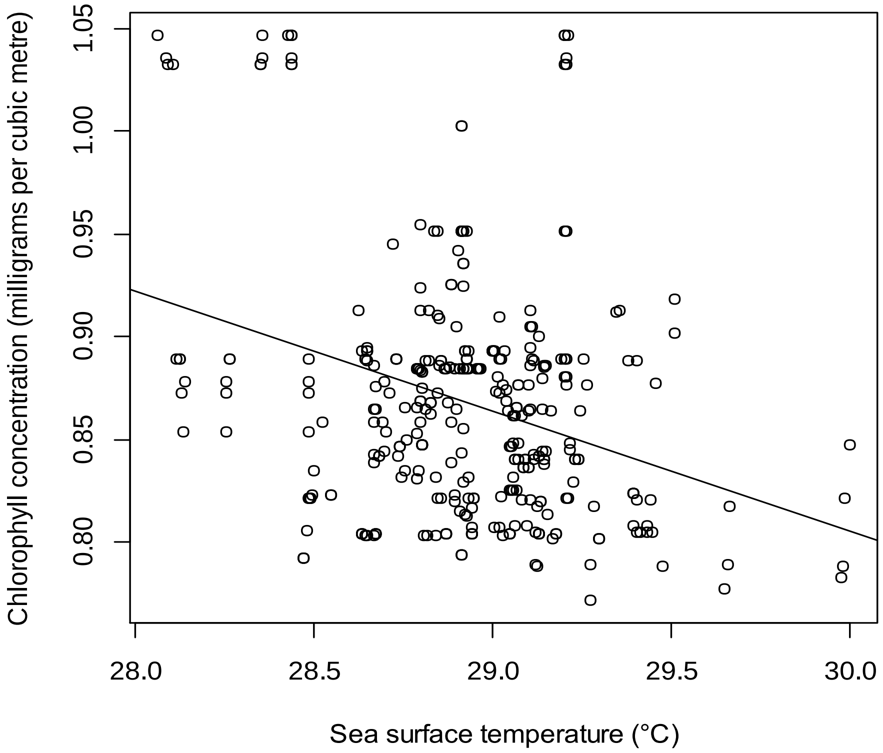

Figure 2. Plot of sea surface temperature compared to chlorophyll concentration over all weeks surveyed at all sites.

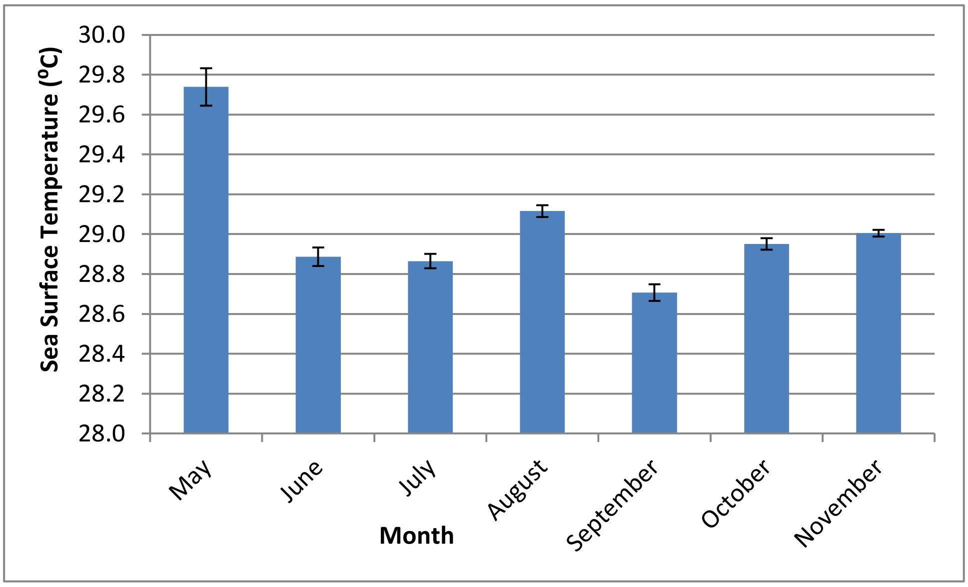

Figure 3. Average sea surface temperature each month over the 3 years.

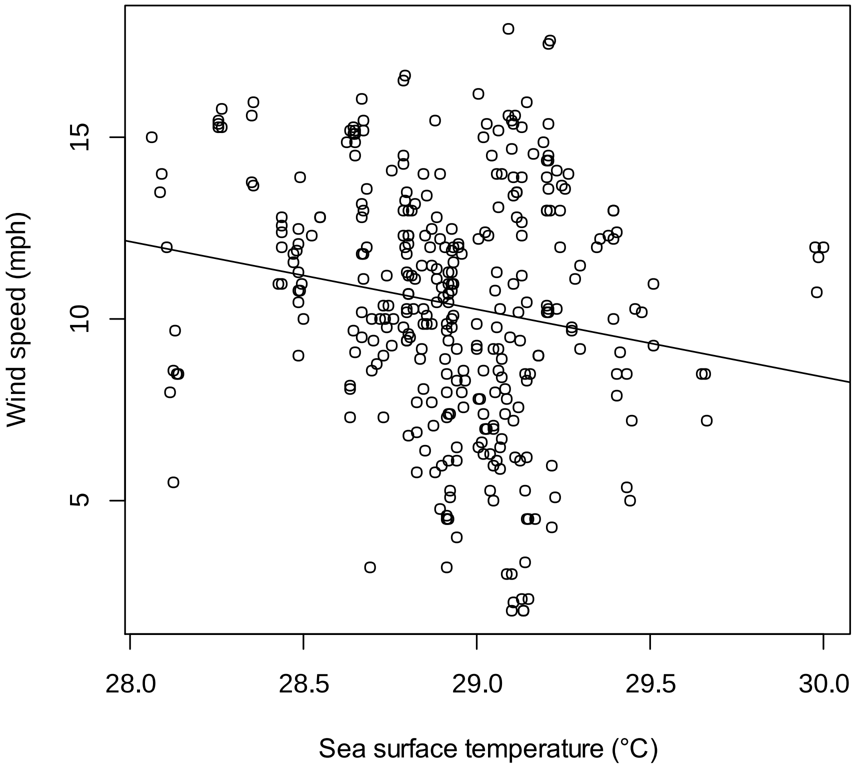

Figure 4. Average wind speed against average sea surface temperature.

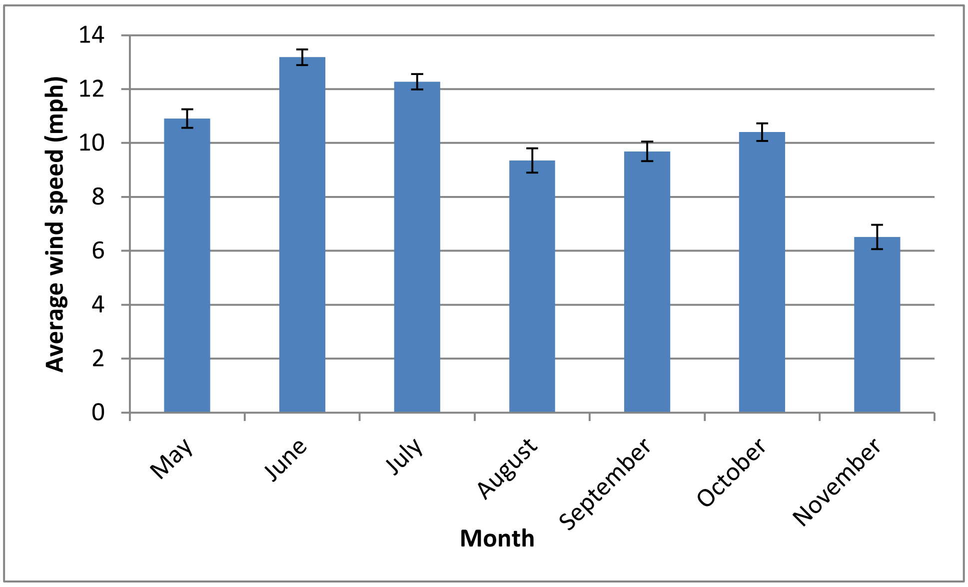

Figure 5. Average wind speed each month over the three years.

Manta rays sightings

The number of manta rays sighted per 15 minutes was significantly different between the sites, with more sighted at Hanifaru Bay and Dharavandhoo Corner and less at Hanifaru Beyru (Table 2a,b&c; Figure 6). The number sighted also had a negative correlation with the chlorophyll a concentration with more manta rays seen in lower concentrations (Table 2a&c; Figure 7). The number sighted was significantly different between the years; considerably more manta rays were sighted in 2012 than the other years (Table 1b; Figure 8). Additionally the number sighted was also significantly different between the months, with fewer sightings in May and more sightings in October (Table 1c; Figure 9).

Table 2. GLMs of the number of manta rays seen per 15 minutes against multiple predictor variables. Model D= deviance explained by the model, E=estimate, D= deviance explained by that variable. Bold type = significant variables following FDR correction (alpha=0.035).

a) Number of manta rays seen per 15 minutes compared to the variables; chlorophyll, site and wind speed	AIC=-842.92 Model D=17.735% **Site: E=-0.0142 D=13.521% P=0.00771^{-10}** **Chlorophyll: E=-0.208833 D=2.428% P=0.00174** Wind speed: E=-0.00162 D=0.463% P=0.169
b) Number of manta rays seen per 15 minutes compared to the variables; year, site, SST and wind direction	AIC=-897.57 Model D=30.296% **Year: E=-0.0365 D=13.879% P=0.00546^{-12}** **Site: E=-0.0141 D=13.322% P=0.00171^{-11}** SST: E=0.0236 D=0.925% P=0.0355 Wind direction: E=0.00901^{-2} D=0.229% P=0.297
c) Number of manta rays seen per 15 minutes compared to the variables; month, site and chlorophyll	AIC=-846.99 Model D=18.710% **Month: E=0.00518 D=1.438% P=0.0151** **Site: E=-0.0139 D=12.780% P=0.00222^{-9}** **Chlorophyll: E=-0.203 D=2.358% P=0.00189**

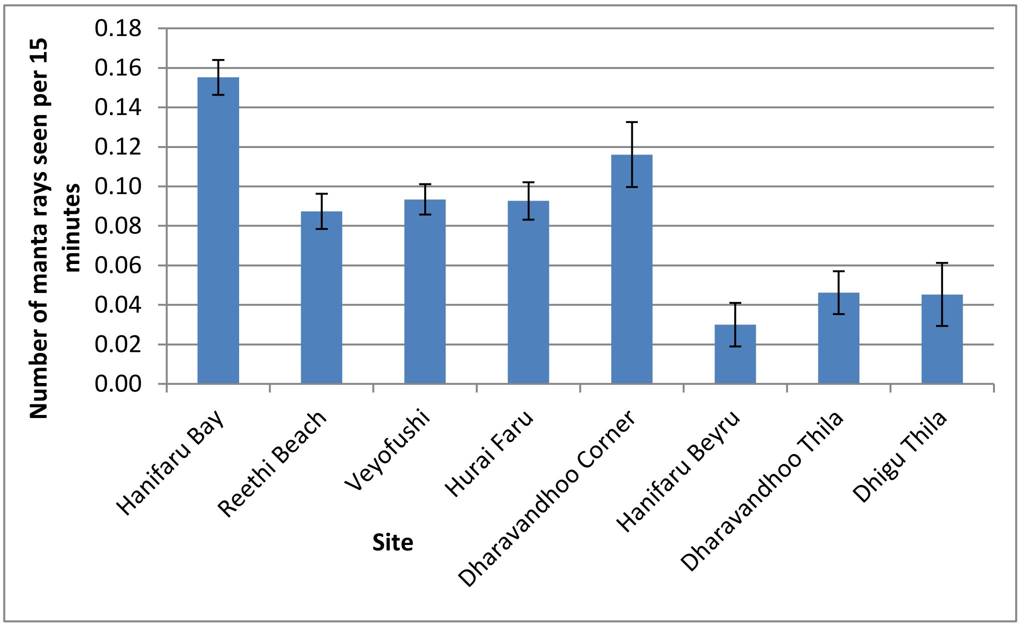

Figure 6. The average number of manta rays seen per 15 minutes at each site.

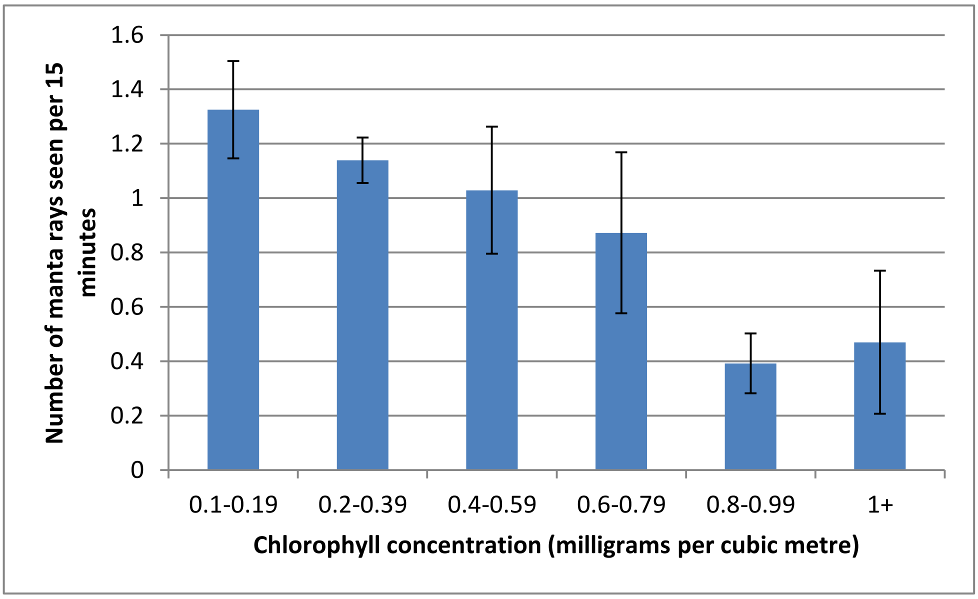

Figure 7. The average number of manta rays seen per 15 minutes compared to chlorophyll a concentration.

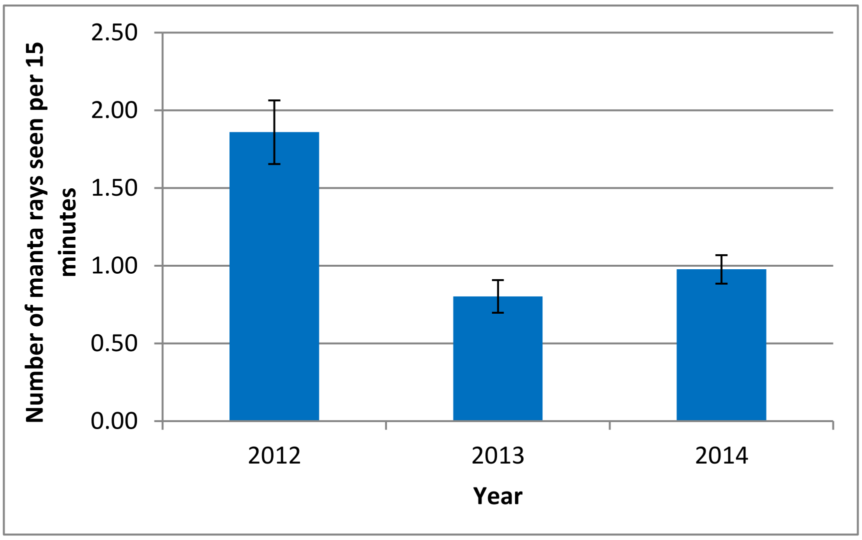

Figure 8. The average number of manta rays seen per 15 minutes each year.

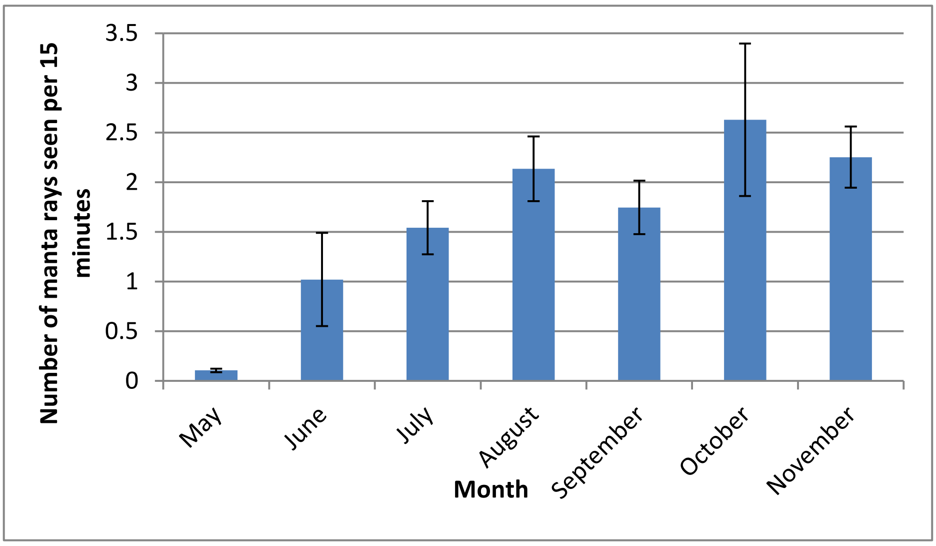

Figure 9. The average number of manta rays seen per 15 minutes each month.

Behaviour

The behaviour of the manta rays was significantly different between sites (Table 3a,b&c). Some sites such as Hurai Faru were exclusively feeding sites and Dharavandhoo Corner was exclusively a cleaning site whereas other at sites such as Dhigu Thila, multiple behaviours were observed. Chlorophyll a concentrations were found to be lower at Dhigu Thila when the manta rays were feeding compared to cleaning and cruising (Table 4). Behaviours were significantly different between the years (Table 3b) including the percentage of visits where manta rays were absent (Figure 10). In 2012 manta rays were seen only feeding or cleaning whereas in 2013 and 2014 they were seen feeding, cleaning and cruising. Additionally a higher percentage of visits in 2013 and 2014 resulted in no manta rays observed than in 2012 (Figure 10).

Table 3. GLMs of the behaviour of manta rays against multiple predictor variables. Model D= deviance explained by the model, E=estimate, D= deviance explained by that variable. Bold type = significant variables following FDR correction (alpha=0.02).

a) Behaviour of manta rays (feeding, cleaning, cruising or absent compared to the variables; site, chlorophyll and wind speed	AIC=1084.7 Model D=20.828% **Site: E=0.290 D=19.426% P=0.002**$^{-13}$ Chlorophyll: E=2.346 D=1.05% P=0.035 Wind speed: E=0.000673 D=0% P=0.973
b) Behaviour of manta rays (feeding, cleaning, cruising or absent compared to the variables; year, site, SST and wind direction	AIC=985.09 Model D=41.176% **Year: E=0.750 D=20.135% P=0.002**$^{-13}$ **Site: E=0.287 D=18.989% P=0.002**$^{-13}$ SST: E=-0.199 D=0.224% P=0.258 Wind direction: E=-0.00157 D=0.236% P=0.247
c) Behaviour of manta rays (feeding, cleaning, cruising or absent compared to the variables; month, site and chlorophyll	AIC=1084.7 Model D=20.488% Month: E=0.00298 D=0.0017% P=0.934 **Site: E=0.291 D=19.320% P=0.002**$^{-13}$ Chlorophyll: E=2.370 D=1.101% P=0.0308

Table 4. The percentage of observations of different behaviours at each site and a Kruskal Wallis or t test (dependant on whether the data was normal or not) to see if there was a significant difference between the chlorophyll concentrations at sites when different behaviours were observed.

Site	Feeding	Cleaning	Cruising	Chlorophyll
Hanifaru Bay	91%	7%	2%	Kruskal-Wallis=3.368 df=2 p=0.186
Reethi Beach	98%	0%	2%	N/A
Veyofushi	98%	0%	2%	N/A
Hurai Faru	100%	0%	0%	N/A
Dharavandhoo Corner	0%	100%	0%	N/A
Hanifaru Beyru	63%	0%	38%	t=-0.423 df=5.850 p=0.688
Dharavandhoo Thila	10%	90%	0%	Kruskal-Wallis= 2.0755 df=1 p=0.150
Dhigu Thila	38%	50%	13%	t=-4.100 df=5.957 p=0.00646

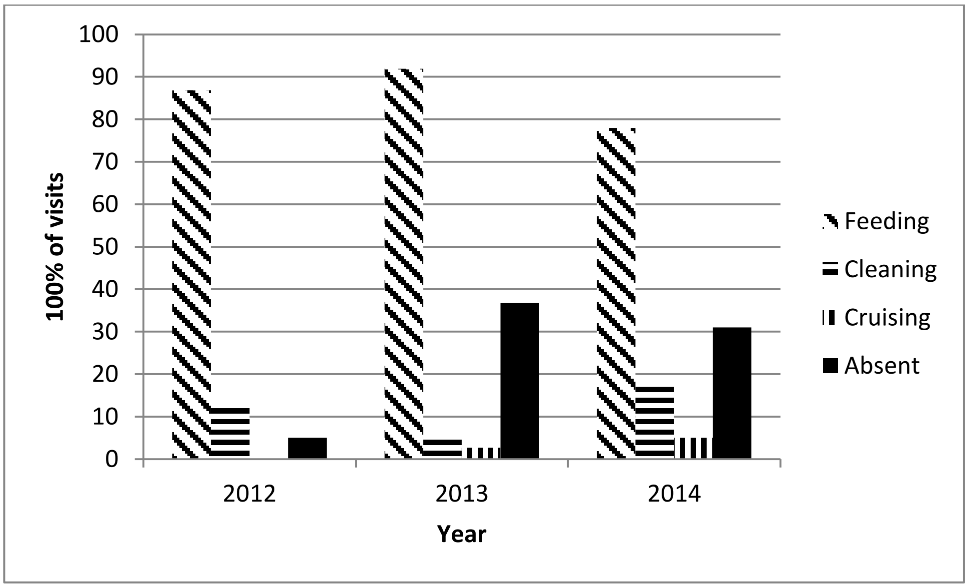

Figure 10. The percentage of visits that each behaviour was dominant each year and the percentage of visits each year where manta rays were absent.

Courtship

None of the predictor variables were significant in any of the models. (Table 4).

Table 5. GLMs of the presence/absence of courtship against multiple predictor variables. Model D= deviance explained by the model, E=estimate, D= deviance explained by that variable.

a) Presence/absence of courtship compared to the variables; site, chlorophyll and wind speed	AIC=83.317 Model D=0.764% Site: E=0.0229 D=0.0224% P=0.896 Chlorophyll: E=0.463 D=0.0079% P=0.939 Wind speed: E=0.0805 D=0.646% P=0.490
b) Presence/absence of courtship compared to the variables; year, site, SST and wind direction	AIC= 85.565 Model D=0.437% Year: E=-0.0776 D=0.0395% P=0.863 Site: E=0.0351 D=0.0514% P=0.843 SST: E=0.359 D=0.129% P=0.755 Wind direction: E=0.00327 D=0.183% P=0.711
c) Presence/absence of courtship compared to the variables; month, site, and chlorophyll	AIC= 83.779 Model D=0.156% Month: E=-0.0336 D=0.0369% P=0.868 Site: E=0.0266 D=0.0303% P=0.880 Chlorophyll: E=1.227 D=0.058% P=0.834

Thermal limit

Although no significant correlation was found between SST and the number of manta rays seen per 15 minutes, to see whether the manta rays had a preference for a certain temperature range the SST data was categorised into increments of 0.25^{o}C. The number of manta rays sighted dropped considerably in temperatures higher than 29.75^{o}C (Figure 11).

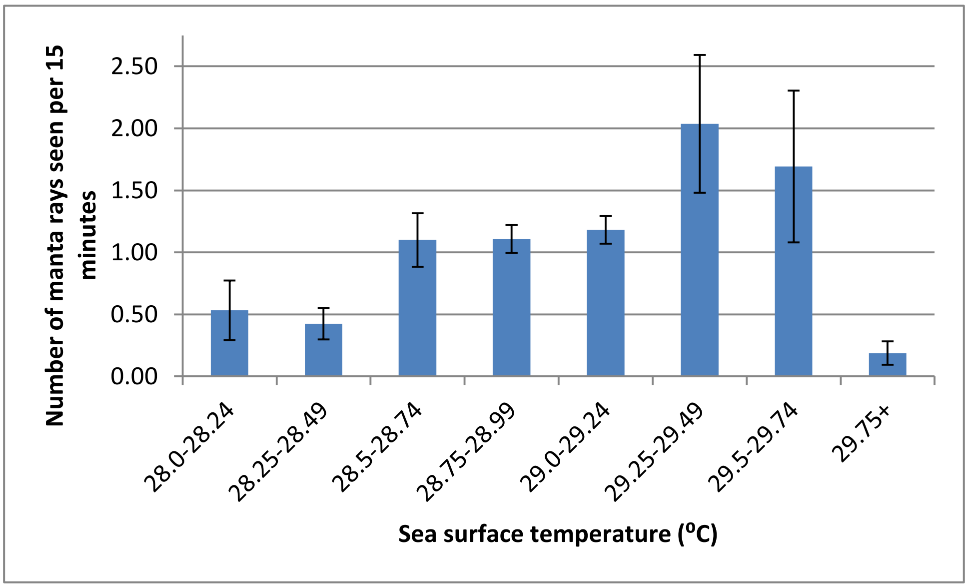

Figure 11. The number of manta rays seen per 15 minutes compared to sea surface temperature.

Discussion

The results showed that the number of manta rays sighted varied between sites, years and months and that more manta rays were seen in weeks where the chlorophyll concentrations were lower. They additionally showed that behaviours also varied between sites and years. The presence of courtship could not be linked to any of the variables in this study but the SST results indicated that manta rays may prefer waters lower than 30^{o}C.

Environmental variables

Chlorophyll

Chlorophyll was negatively correlated with SST (table 1 and figure 2) which has been observed in other studies, indicating the euphotic zone of colder water contains more nutrients which allow phytoplankton to bloom showing high concentrations of chlorophyll a (Solanki *et al.*, 2001 & Gremillet *et al.*, 2008). However, in the Black Sea, chlorophyll levels were found to increase with SST but a month behind (Kavak & Karadogan, 2012). It was concluded that the relationship between chlorophyll and SST may be different if the area is affected by upwellings or not. Upwellings in the Maldives occur on the windward side of the atolls and once the currents reach the leeward side (the location of the sites for this study), primary productivity is reaching its peak from the nutrient input, which allows the large manta populations found at these sites to flourish (Manta Trust, 2011).

Chlorophyll had a significant difference between months but not after FDR correction. Chlorophyll was low in May, highest in June, decreased in July and stayed relatively constant until October, then increased in November. This was due to the changing monsoons; the south west monsoon begins in late May (Tan *et al.*, 2006) meaning that the majority of May is between the two monsoons. In southern Bay of Bengal chlorophyll concentrations were lower in the inter-monsoon periods (Dey & Singh, 2003). In June the south west monsoon has properly begun, causing the currents to flow east bringing nutrients to the east side of Baa atoll, causing the bloom in phytoplankton. The increase in chlorophyll concentrations in November is then likely due to the onset of the north east monsoon although the chlorophyll levels did not increase to those seen in June as during the north east monsoon, the eastern side of Baa atoll becomes the upstream side and receives clear oceanic water, reducing the potential for a large plankton bloom (Anderson *et al.*, 2011).

There was found to be no significant difference between chlorophyll concentrations and year, site, wind direction or speed. However, when retrieving the chlorophyll data from NOAA Ocean Watch, some of the sites fell into the same square as some sites were too close together for the resolution of the data, the eight sites surveyed fell into 5 different squares (see appendix one). This meant that some sites such as Hanifaru Bay and Hanifaru Beyru both showed the same chlorophyll concentrations whereas in reality they likely had slightly different concentrations.

SST

The difference in average wind speed between months (figure 3) was due to the monsoons. Kench *et al.* (2006) also found wind speed to be strongest in June, drop in August, rise slightly and drop again in November. This is because the crossovers between monsoons have the lowest wind speeds, those months being April/May and November (Kench *et al.*, 2006). According to Windfinder.com the average wind speed for August in the Maldives is lower than July and September and June has a considerably higher probability of having wind speeds of over 15mph compared to the following months (Windfinder, 2017). SST was found to have a significant negative correlation with wind speed, showing the stronger the wind speed, the lower the SST (table 1). This could be because stronger winds move more surface water creating upwellings bringing colder water to the surface (Gremillet *et al.*, 2008). SST was highest in May with an average of 29.74°C, the other months ranged on average between 28.71°C and 29.12°C. This was likely because the South West monsoon had yet to begin, meaning there were no upwelling's bringing cooler water to the surface (Anderson *et al.*, 2011). This links to the chlorophyll concentration results which showed lower concentrations in May because there were not enough nutrients in the euphotic zone to cause a bloom of phytoplankton. SST was not significantly different between the years, wind direction or the sites. However the SST has the same limitations with regard to site as the chlorophyll data because it had the same resolution, giving sites close to each other the same SST when in reality they could have been slightly different. Therefore it is difficult to know whether some sites were more affected by cooler currents than others which could have been having an effect on the number of manta rays frequenting that site.

Wind direction

Wind direction was different between the months surveyed however it was mainly either a westerly wind or west north west, becoming more north west in September. This was to be expected as the surveys were only done in the south west monsoon season. No other variables were significantly correlated with wind direction and as the wind direction model only explained 4.6% of the deviance it can be concluded that in this study wind direction was not a key variable.

Wind speed

Wind speed was significantly different between months. It was highest in June and July and lowest in November (figure 3), this is discussed above with relation to the SST model. Wind speed was also significantly different between years; it was lowest in 2012 and highest in 2014. This could potentially be due to the Indian Ocean Dipole, as 2012 was a positive dipole year (Marsac, 2013). Positive dipole years are characterised by weaker westerly winds across the Indian Ocean (Bureau of Meteorology, 2017). Wind speed was not significantly different between sites however this was to be expected as the sites were all in relatively close proximity to each other.

Manta ray sightings

Year

Significantly more manta rays were seen per 15 minutes in 2012 than the other years. This could not be contributed to the data collectors going to sites that consistently had more numbers of manta rays such as Hanifaru Bay and Dharavandhoo Corner (figure 5) in 2012 as these sites were visited more often in 2014. It could not be contributed to data collectors spending more time at sites in 2012 as on average in 2012 they spent 4 hours at a site, in 2013 they spent 4 hours 45 minutes and in 2014 they spent 3 hours 30 minutes. Year was only correlated with wind speed showing lower wind speeds on average in 2012 which does not concur with other studies that have found more manta rays when there were consistent strong winds and fewer sightings at low wind speeds (Stevens and Brooks, 2012). This indicates that another variable was having more influence on the manta rays than the wind speed in 2012.

Site

More manta rays were seen per 15 minutes at sites such as Hanifaru Bay where on average 0.15 manta rays were seen per 15 minutes and a maximum of 7.71, whereas sites such as Dhigu Thila, only 0.05 manta rays were seen with a maximum of 3.2. None of the environmental variables were significantly different between sites; therefore it may be constant physical features of the sites which make some of them more favourable than others to manta rays, rather than the changeable variables. The feeding sites where more manta rays were seen per 15 minutes; Hanifaru Bay, Reethi Beach, Veyofushi and Hurai Faru, all have shallow water or land to the east of them, meaning zooplankton brought in by the eastern flowing current could get trapped and build up in those locations attracting the larger numbers of manta rays. Dharavandhoo Corner was the cleaning site with the most manta rays seen per 15 minutes and it is located on the east side of an island meaning it would be sheltered from the east flowing current. Rohner *et al.* (2013) studied the environmental variables influencing the sightings of manta rays at cleaning stations in Mozambique and found fewer manta rays at the cleaning stations when the currents were strong compared to medium or light. They concluded that strong currents are too energetically costly for manta rays to hold their position above the reef to be cleaned as well as being difficult for the cleaner fish to stay on the manta ray against the current. Therefore the sheltered location of Dharavandhoo Corner compared to Dharavandhoo Thila and Dhigu Thila may explain why more manta rays were seen there.

Chlorophyll

There was a significant negative relationship between the number of manta rays seen per 15 minutes and the chlorophyll concentration (Figure 7). This may be because the manta ray aggregations were due to the abundance of zooplankton which had already consumed the bloom of phytoplankton meaning chlorophyll concentrations would be low (Boyce *et al.*, 2010).

Month

Significantly fewer manta rays were seen in May than the other months (figure 6), this was because May is the changeover to the south west monsoon and the manta rays had yet to migrate to the leeward side of the atoll (Anderson *et al.*, 2011). The number of manta rays sighted generally increased as the season went on, decreasing slightly at the changeover to the north east monsoon in November (Shankar *et al.*, 2002). At the start of the season, June and July, this could indicate a gradual return of manta rays from Ari atoll or Raa atoll where the manta rays migrate to during the north east monsoon (Manta Trust, 2011). However the peak number of manta ray sightings in October was unexplained by the data in this study.

SST

Although there was no significant correlation between the numbers of manta rays seen per 15 minutes and SST, manta rays are thought to have an upper thermal limit of 30^{o}C (Dewar *et al.,* 2008). In my study the average number of manta rays seen increased up to 29.5^{o}C when 2.04 manta rays were seen per 15 minutes then decreased, significantly dropping in temperatures above 29.75^{o}C when only 0.19 manta rays were seen per 15 minutes (figure 7). Therefore the results of this study concur with Dewar *et al.* (2008).

Wind

There was no significant correlation between the number of manta rays and the wind direction or the speed. A link between manta ray sightings and wind direction would potentially have been seen if data had also been collected in April and December.

Behaviour

Year

In 2012 the dominant behaviours were either feeding (87%) or cleaning (13%), in 2013 all three behaviours, feeding (92%), cleaning (5.5%) and cruising (2.5%) were observed and in 2014, feeding was the dominant behaviour for 78% of the weeks, cleaning for 17% and cruising for 5%. The higher percentage of cleaning occurring in 2014 is likely due to the data collectors frequenting the cleaning station Dharavandhoo Corner significantly more in 2014 than the other years. However it is unclear why manta rays were seen cleaning more often in 2012 than 2013.

Site

Some sites were either exclusively cleaning or feeding sites whereas others showed manta rays performing multiple behaviours. This could not be contributed to the environmental variables in this study but is likely to do with the location and physical features of the sites as mentioned in the manta rays sightings section above. Over a longer study period it would be possible to get a better analysis of the changes in variables within a site when manta rays are performing different behaviours.

There was no significant correlations between the behaviour observed and the other variables included in the model however better results could be achieved if the data could have been studied on a daily basis rather than weekly like in studies such as Jaine *et al.*, (2012).

Courtship

None of the predictor variables were significantly different when courtship was observed however in the 3 years that were studied, there were only 8 weeks where courtship was observed. Therefore there was probably not enough data to show any correlations, highlighting the need for a longer term study to be done on the courtship behaviour of manta rays in the Maldives. Marshall and Bennett (2010) studied the reproductive ecology of manta rays in Mozambique and found fresh mating wounds from October to January and fresh reproductive wounds in November and December, indicating a seasonal link. Marshall and Bennetts study was done over a longer time period and all year round which highlights the potential need for data to be analysed year round by including sighting of individuals that were seen in Baa atoll in the southwest monsoon and in the surrounding atolls in the north east monsoon so as to effectively monitor the population when they migrate to the surrounding atolls in the north east monsoon (Anderson *et al.*, 2011).

Limitations

There was possibly a limitation with the way the data was collected which although controlling for effort overcame this partially, there was still potentially a bias against sites where high numbers of manta rays were seen. This was because the data collectors tended to spend more time at these sites, reducing the number of manta rays seen per 15 minutes in the data. If they had spent less time at the site they still may have seen a large number of mantas and this would have changed the data meaning more manta rays were seen per 15 minutes. Likewise at sites where the data collectors only spent 15-30 minutes and saw a small number of manta rays, if they had stayed longer they might not have seen any more, reducing the number seen per 15 minutes in the data. Therefore to get a more accurate data set, the time that the maximum number of manta rays seen should be recorded and any further time spent at the site should be recorded separately.

Conclusion

Although there were limitations with the data in this study, it is clear that the number of manta rays and their behaviour varied spatially and temporally. The location, size and behaviour of manta ray aggregations in Baa atoll are most likely influenced by upwelling's and currents and therefore the location of the sites is key. To increase our understanding of why some sites attract manta rays more than others, longer term studies looking at daily data are needed, however chlorophyll a concentration is potentially not the ideal way to measure food availability for manta rays. To accurately study food availability for manta rays on such a fine scale of daily movements, it may require physical sampling of the water at the sites to measure the zooplankton concentration. Additionally further studies are required into the temperature tolerance of manta rays with regard to rising sea surface temperatures. Hanifaru Bay was declared a Marine Protected Area in 2009 (Cagua *et al.,* 2014) but as this study shows that Hanifaru Bay is almost exclusively a feeding site, it highlights the potential need to look at management measures to be put in place on cleaning sites where manta rays are frequently sighted.

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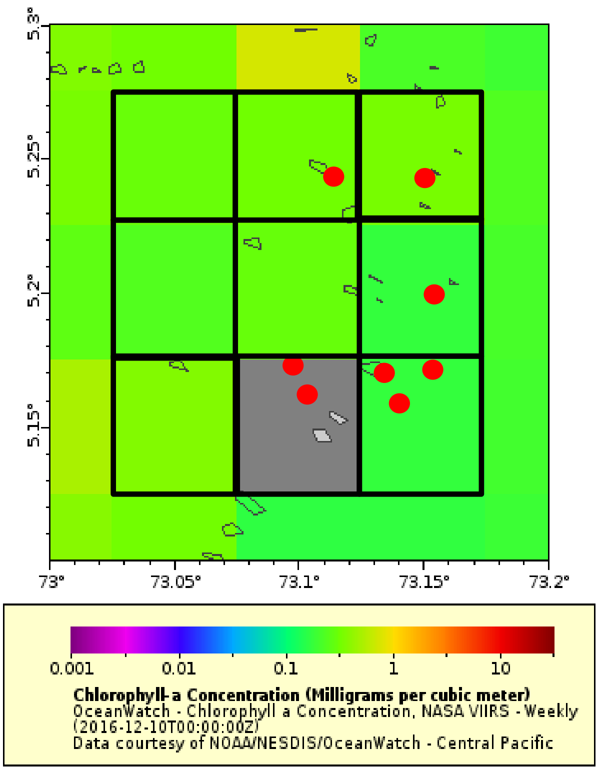
Appendix one



The location of the study sites in relation to the resolution of the chlorophyll data.