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Assessing the environmental and biological variables that make South Ari Atoll Marine Protected Area (SAMPA) a world renowned whale shark aggregation site

Jefferson, 2017

Tamlin Jefferson
Exam number: Y3845358

Disclaimer

I hereby declare that this dissertation is my own original work and has not been submitted before to any institution for assessment purposes. Furthermore, I have acknowledged all sources used and have cited these in the reference section.

Tamlin Jefferson, 18/09/2017

Acknowledgements

I would like to acknowledge the support provided by James ‘Jim’ Hancock and Richard Rees, the directors of the Maldives Whale Shark Research Programme (MWSRP). They provided scientific guidance as well as the primary data used in this study. I would also like to thank all those who have worked for and volunteered with the MWSRP since its inception, their hard work and consistent data collection allowed this research project to be undertaken. I would also like to acknowledge the support of my project supervisors, James Hancock from the MWSRP and Bryce Beukers-Stewart from the University of York. Finally, I would like to thank all those whom I have cited for their diligent work and research, without the scientific background and data used from various institutions this study would not have been possible.

Abstract

Whale sharks (*Rhincodon typus*) typically aggregate in response to seasonal increases in prey abundance, with phytoplankton blooms as well as fish and coral spawning events attracting large numbers of sharks. However, the whale sharks of South Ari Atoll Marine Protected Area (SAMPA) show extraordinary site fidelity, with a predictable year round population and no seasonal peak in aggregations. Whale sharks are slow to reach sexual maturity and vulnerable to overexploitation, which has resulted in a decline in global populations by >50% over the last 75 years. This study assesses the environmental and biological variables driving whale shark aggregations at SAMPA in order to improve whale shark conservation strategies. The whale shark encounter and environmental data used in this study were collected by the MWSRP team from the 1st of January 2014 to the 18th of April 2017. Surveys were conducted from Dhigurah to Rangali along the epipelagic reef fringe in a local vessel. A mean of whale sharks per day (shark encounters/search effort) and 12 environmental variables were calculated to allow for accurate comparisons between data using a Gaussian Generalised Linear Model (GLM). Of these variables, chlorophyll a (P=0.0217) and current strength (P=0.0058) were found to have a significant relationship with mean whale sharks per day (α=0.026). The environmental and biological variables analysed were found to affect the year round aggregation of whale sharks at SAMPA, but the primary drivers of site fidelity remain unknown.

1. Introduction

1.1 Background

The whale shark, *Rhincodon typus*, is a filter-feeding cartilaginous elasmobranch, capable of growing over 18m in length (Chen *et al*, 1997; Compagno, 2001; Sequeira *et al*, 2013). *R. typus* are the largest extant fish, and like other large marine megafauna, are characterised by slow growth rates, late sexual maturity and infrequent reproduction (Riley *et al*, 2010; Pierce & Norman, 2016). Whale sharks are particularly vulnerable to overexploitation due to their biological characteristics, tendency to swim near the surface, and transboundary migratory behaviour (Riley *et al*, 2010; Sequeira *et al*, 2013; Vignaud *et al*, 2014). Furthermore, targeted pelagic fishing, by-catch, incidental capture and boat collision are the major causes of mortality for the species (Casey *et al*, 1992; Colman, 1997; Li *et al*, 2012).

In 2003, *R. typus* was added to Appendix II of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). A number of countries; India, the Maldives, the Philippines, Thailand, Belize, Honduras, Mexico, U.S.A, Australia and Taiwan in 2008, have moved to regulate, restrict and prohibit the targeted fishing and sale of *R. typus* products (Chen & Phipps, 2002; Hausfather, 2004; Norman, 2004). Due to the migratory nature of whale sharks, enforcing regulations across international boundaries leaves the species vulnerable in areas of low enforcement with limited or no protection (Li *et al*, 2012; Eckert *et al*, 2002).

The majority of states located within the range of *R. typus* (figure 1) do not have a target fishery for the species, but there is a growing demand for meat and fins within the Chinese market (Clarke, 2004). Li *et al* (2012) notes that “One of the largest processing companies (Wenzhou Haideli Co. Ltd) stated that in excess of 1000 *R. typus* are landed annually in Hainan”. This shows signs of an evolving target fishery in China and highlights the challenges faced to conserve *R. typus* globally. Last year (2016), the International Union for the Conservation of Nature (IUCN) upgraded the status of *R. typus* from Vulnerable to Endangered on the IUCN Red List of Threatened Species. This followed research highlighting the decline in global populations by >50% over the last 75 years due to overexploitation (Pierce & Norman, 2016).

Despite an increase in *R. typus* research over the last twelve years (Irvine & Keesing, 2007; Sequeira *et al*, 2013), little is known of whale shark distribution, migration patterns and connectivity (Sequeira *et al*, 2012), as well as behavioural ecology (Brunnschweiler *et al*, 2009), reproduction and life history (Rowat & Brooks, 2012). Consequently, it is difficult to protect the species against overexploitation (Stewart & Wilson, 2005) and deduce the impact of targeted fishing, by-catch and other anthropogenic induced mortality on whale shark populations (Li *et al*, 2012). In order to improve current *R. typus* conservation and management efforts, a broader understanding of the variables influencing whale shark distribution and aggregations is imperative (McKinney *et al*, 2012; Rowat & Brooks, 2012).

1.2 Distribution and aggregations

Whale sharks have a circumglobal distribution within tropical, sub-tropical and warm temperate waters between 30°N and 35°S, excluding the Mediterranean (Compagno, 2001; Last & Stevens, 2009). Compared with their seasonal aggregations, which are well known, their pelagic distribution and potential range is poorly understood (Colman, 1997; Castro *et al*, 2007; Brunnschweiler *et al*, 2009) and based primarily on sightings from fishing boats (Sequeira *et al*, 2012).

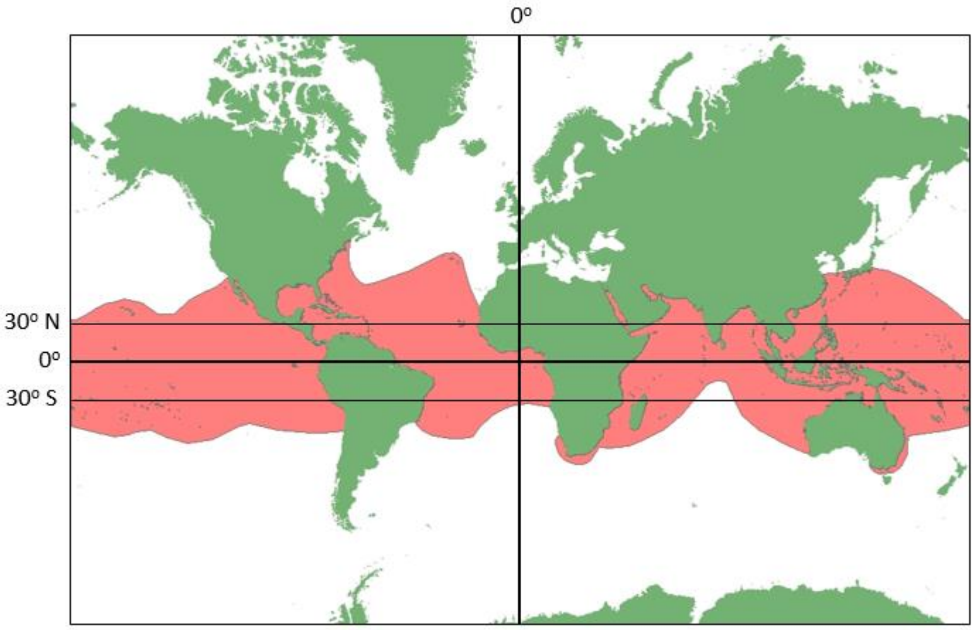


Figure 1: Global range of R. typus – red (Spatial data from IUCN Shark Specialist Group, 2016). Vignaud et al (2014) suggest that subpopulations within the Atlantic and Indo-Pacific are functionally separate. Over the last 75 years the Atlantic subpopulation has seen a decline of *≥30% (Sequeira et al, 2014) and the Indo-Pacific population a decline of >50%, estimated at 63% (Pierce & Norman, 2016). Counts, population model estimates and habitat availability infer that the Indo-Pacific population harbours 75% of individuals, with 25% in the Atlantic subpopulation (Pierce & Norman, 2016).*

It is widely accepted that the range of *R. typus* is constrained by the sea surface temperatures (SST) they can tolerate (Sequeira *et al*, 2014), with individuals rarely spotted in areas below 21°C (Colman, 1997; Duffy, 2002; Afonso *et al*, 2014; Tomita *et al*, 2014). Sequeira *et al* (2013) notes that warming ocean temperatures may already be affecting *R. typus* distributions. Sharks have been documented as far north as the Bay of Fundy, Canada (Turnbull & Randell, 2006) and the Sea of Okhotsk, Japan at

44°N (Tomita *et al*, 2014), and as far South as North East New Zealand, >35°S (Duffy, 2002) and Victoria, Australia, 37°S (Wolfson, 1986).

Although *R. typus* are a largely solitary species (Hearn *et al*, 2016; Barbosa-Filho *et al*, 2016), feeding aggregations are increasingly being observed, suggesting they live a more gregarious life than previously thought (de la Parra Venegas *et al*, 2011). These aggregations, sometimes hundreds strong (de la Parra Venegas *et al*, 2011; Ramírez-Macías *et al*, 2012), are known to occur seasonally at over twenty coastal sites worldwide (Colman, 1997; Eckert & Stewart, 2001; Heyman *et al*, 2001; Stewart & Wilson, 2005; Rowat *et al*, 2007, Riley *et al*, 2010; Rowat & Brooks, 2012; Robinson *et al*, 2013).

Figure 2: Aerial photograph of R. typus aggregation in Afuera, North Mexicon Caribbean (Reyes, 2009). Note the four boats and approximately 220 whale sharks (de la Parra Venegas et al, 2011).

Aggregations typically correlate with seasonal food pulses (Graham *et al*, 2006; Meekan *et al*, 2006; Rowat *et al*, 2007; Rowat *et al*, 2009) as shown by those at Christmas Island, Belize and Ningaloo reef, where they time their arrival with mass crab (Hobbs *et al*, 2009), snapper (Graham & Roberts, 2007) and coral spawning events (Taylor, 1996). When prey availability decreases or SST falls (Hacohen-Domené *et al*, 2015), *R. typus* disperse to forage elsewhere (Sequeira *et al*, 2013; Cagua *et al*, 2015).

Aggregation connectivity and migration pathways remain mostly unknown (Castro *et al*, 2007; Schmidt *et al*, 2009), although recent studies using telemetry and satellite tracking have shown some connectivity between aggregation sites, as well as shark dispersion routes (Gunn *et al*, 1999; Eckert & Stewart 2001; Gifford *et al*, 2007; Brunnschweiler *et al*, 2009; Cagua *et al*, 2015).

Whale shark ecology is most advanced within the Indian Ocean (Sequeira *et al*, 2013) with substantial research showing high site mobility (Wilson *et al*, 2001; Rowat *et al*, 2007; Robinson *et al*, 2013; Berumen *et al*, 2014) in addition to site fidelity in certain locations (Riley *et al*, 2010). In the Maldives, *R.typus* are perceived to have a 'semi-annual residency pattern' as their distribution shifts West during December to April and East during May to November (Donati *et al*, 2016). However, South Ari Atoll in the Maldives is a unique study site due to its year round residency of whale sharks (Riley *et al*, 2010; Cagua *et al*, 2014; Donati *et al*, 2016). Therefore, the site represents an excellent opportunity to further scientific understanding regarding the environmental and biological factors driving whale shark site fidelity and aggregations.

1.3 Environmental and biological variables

A number of environmental and biological variables influence whale shark distribution and aggregations (Rowat & Brooks, 2012; Rohner *et al*, 2013; Sequeira *et al*, 2013). One of the primary environmental drivers is sea surface temperature (SST), and in the Indian Ocean *R. typus* habitat suitability is mainly correlated with spatial variations in SST, with 90% of whale sharks showing a strong preference for SST between 26.5 and 30°C (Sequiera *et al*, 2012).

R. typus are spotted at the limit of their range only during unusually warm summer and autumn periods when SST is at its highest (Ebert *et al*, 2004; Turnbull & Randell, 2006; Tomita *et al*, 2014). Additionally, the location of periodically warmer currents, such as the 22°C isotherm in the Azores, have been shown to affect the number and distribution of *R. typus* (Afonso *et al*, 2014). In the North Mexican Caribbean, large *R. typus* aggregations show strong connectivity with SST, peaking during the highest levels of SST and reducing in numbers as SST drops (Cardenas-Palomo *et al*, 2010).

Whale shark abundance and distribution are also driven by oceanographic features (Eckert & Stewart, 2001; Duffy, 2002; Sleeman *et al*, 2010a; Rowat & Brooks, 2012; Macena & Hazin, 2016). Currents, eddies and thermal fronts increase environmental productivity resulting in higher prey abundance (Wilson *et al*, 2001; Hoffmayer *et al*, 2005; Hsu *et al*, 2007), such as zooplankton and fish, that accumulate around these features (Balch & Byrne, 1994). *R. typus* have a varied diet, feeding on small organisms such as plankton, fish eggs, and coral spawn (Hacohen-Domené *et al*, 2006; Taylor, 2007; Robinson *et al*, 2013), as well as larger nektonic animals such as small species of fish and squid (Last & Stevens, 1994; Duffy, 2002; Hacohen-Domené *et al*, 2015). Chlorophyll a, a measure of phytoplankton concentration (Sequeira *et al*, 2014), has been measured using satellite imagery to successfully predict whale shark aggregations (Taylor & Pierce, 1999; McKinnery *et al*, 2012).

Sites with varying bathymetry; seamounts, canyons and steep shelfs, such as those found at the Galapagos Islands, St Helena, the Maldives, the Mozambique channel and the Gulf of Mexico amongst others, attract whale shark aggregations due to the nutrient rich upwellings these features create

(Brunnschweiler *et al,* 2009; Rowat *et al*, 2011; McKinney *et al*, 2012). Studies using remote sensing devices have shown that *R. typus* regularly feed at great depths in bathymetrically unrestricted habitats, descending to a maximum of 1928m (Berumen *et al*, 2014; Tyminski *et al*, 2015). Following deep foraging dives in cooler waters (Brunnschweiler *et al*, 2009), sharks are frequently spotted close to the surface in order to aid thermoregulation (Thums *et al*, 2012), thus favouring areas of higher SST. This diving behaviour implies that seasonal aggregations can occur in coastal and surface waters with low productivity (Brunnschweiler et al, 2011).

Lunar cycles are also an important environmental variable, as corals, fish, squid and other *R. typus* prey often spawn and aggregate during specific times of the lunar cycle (Robinson *et al*, 2013). At Gladden Spit in Belize, snapper spawn annually during the full moon phase between April and May (Heyman *et al*, 2001) attracting a large aggregation of *R.typus* (Graham & Roberts, 2007). In South Ari Atoll, acropora corals spawn en masse annually between March and April, again initiated by the full moon (Loch *et al*, 2002). At Ningaloo reef, following the full moon, mass spawning of scleractinian corals occurs annually between March and April, attracting one of the largest and best studied whale shark aggregations (Taylor, 1996; Taylor & Pearce, 1999; Wilson *et al*, 2001; Sleeman *et al*, 2010a).

As highlighted *R. typus* aggregations and distribution are predominately driven by factors governing SST and food availability (Colman, 1997; de la Parra Venegas *et al*, 2011; Sequeira *et al* 2012; Rowat & Brooks, 2012). However, at South Ari Atoll a unique year-round aggregation of whale sharks persists (Riley *et al*, 2010).

1.4 Aims

This report investigates the environmental and biological variables that make South Ari Atoll Marine Protected Area (SAMPA) a year round aggregation site for whale sharks.

In doing this the core objectives are:

- Determine the environmental and biological variables present at SAMPA.
- Investigate the relationship of variables with the frequency of whale shark encounters.
- Rank the most important variables to whale shark site fidelity.

Whale sharks are in need of increased governmental protection but only by understanding where and why they aggregate can accurate management strategies be formed to effectively conserve the species (Donati *et al*, 2016).

2. Methods

2.1 Study site

The South Ari MPA is the largest MPA in the Maldives (figure 3), covering a total area of 42km^2 (Cagua *et al*, 2014) and situated between 3°38’10N and 3°32’15N, and 72°42’18E and 72°55’58E (Rasheed *et al*, 2016). Designated in 2009 to ‘protect and preserve a Maldivian aggregation of whale sharks’ (Cagua *et al*, 2014), to date neither a management plan nor regulation of the MPA have been realised (Rasheed *et al*, 2016). The MPA extends from the North West of Rangali to the North East of Dhigurah, extending 1km seaward from the reef crest (Rasheed *et al*, 2016).

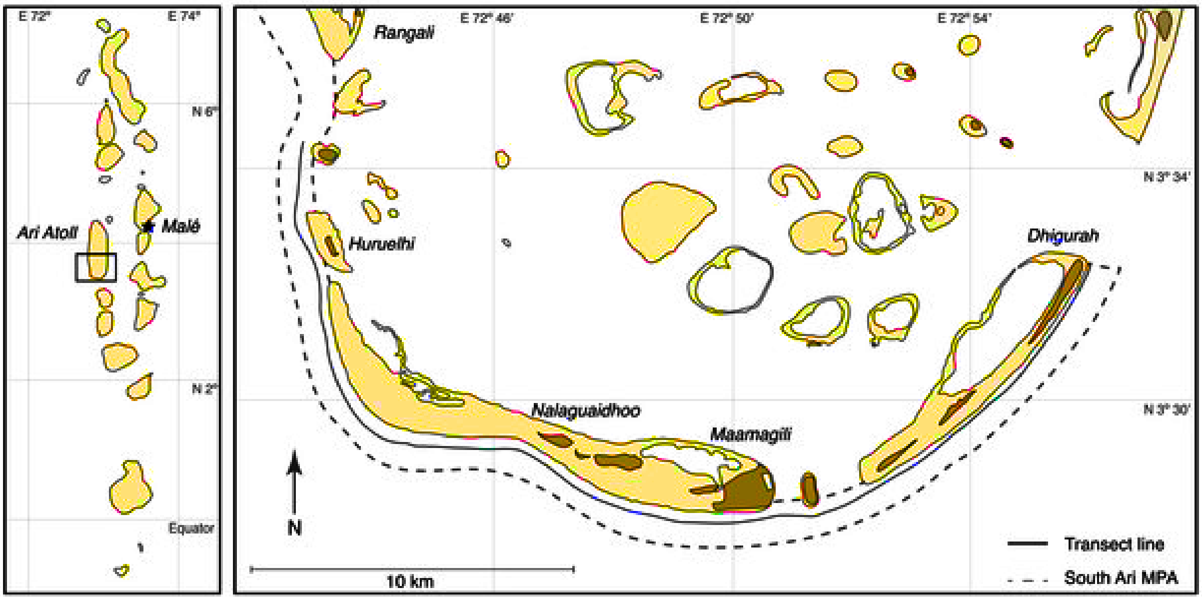


Figure 3: The Maldives and South Ari Atoll Marine Protected Area (Cagua et al, 2014). Land – brown, reef – yellow, MPA - dotted line, typical survey route – solid line. The MWSRP was previously based at Rangali in the North West but since 2014 has been located at Dhigurah, resulting in a shift in search effort within the MPA.

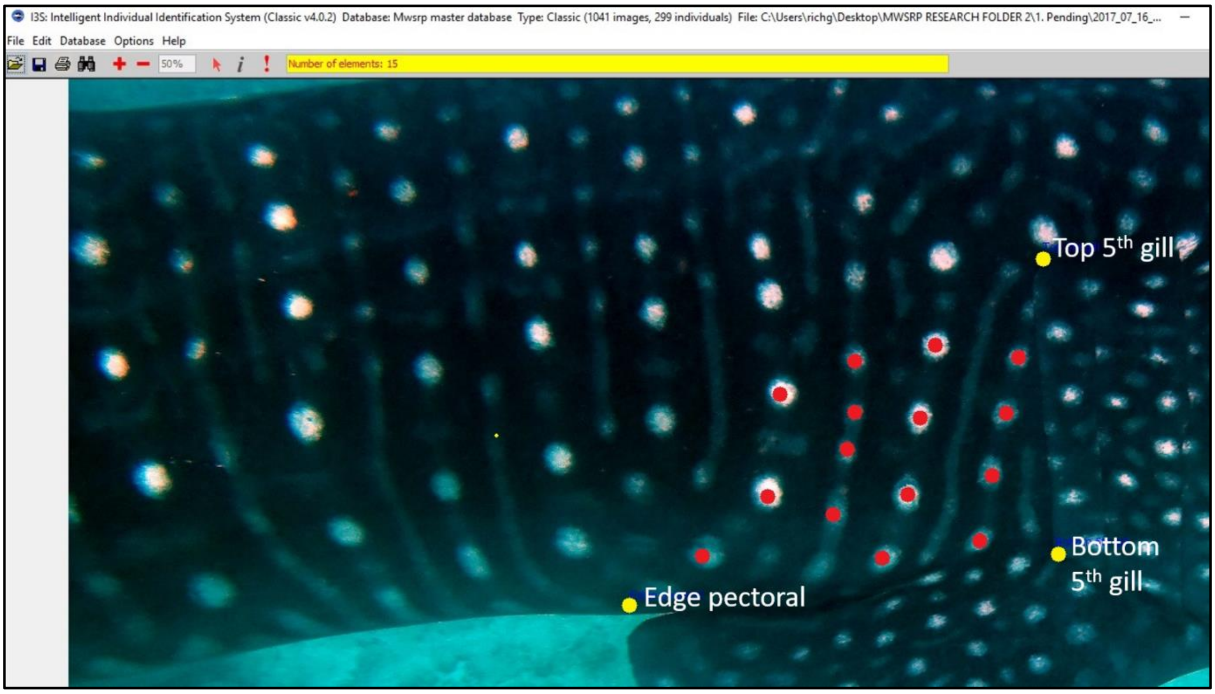
The Maldives and South Ari Atoll are influenced by two monsoon seasons which control the environmental variables and primary productivity at SAMPA (Anderson *et al*, 2011). The Northeast (NE) monsoon is dominant from November to April, and the Southwest (SW) monsoon from May to October (Anderson *et al*, 2011).

2.2 Data collection

The whale shark encounter and environmental data used in this study were collected by the MWSRP from 01/01/14 to 18/04/17. Surveys were conducted from Dhigurah to Rangali along the reef within SAMPA (see figure 3) in a 15.1m wooden hulled, motorised vessel (Riley *et al*, 2010). Surveying began at approximately 9am and finished at 4pm five days per week. *R. typus* were purposely searched for visually throughout this time period by the crew, volunteers and staff of the MWSRP.

During my placement I helped collect data in the field. When a shark was encountered, photos from above the shark, the pelvic fins from below, both sides of the animal, and any injuries and scarring were captured in order to ascertain its identity. A variety of physical details were recorded about the shark, as well as information about the encounter. Additionally, environmental variables were recorded in detail (appendices, figures 18) and the GPS location was noted. Further environmental variables were recorded daily at three GPS locations staggered along the MPA, environmental stations A, B and C (appendices, figure 16).

Shark photographs were analysed using I^{3}S software to determine the identity of each shark (figure 4). Each side shot was analysed by assessing each individual's unique spot pattern behind the 5th gill slit (Meekan *et al*, 2006). Firstly, the top and bottom of the 5th gill and the edge of the pectoral were selected. Secondly, at least twelve individual spots were selected within these boundaries, as shown by the exaggerated dots below.



I3S: Intelligent Individual Identification System (Classic v4.0.2) Database: Mwsrp master database Type: Classic (1041 images, 299 individuals) File: C:\Users\richg\Desktop\MWSRP RESEARCH FOLDER 2\1. Pending\2017_07_16_...

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Figure 4: I³S (Interactive Individual Identification System) software used for matching sharks to a database of known individuals based on their unique spot patterns.

The I3S software then automatically searches its database for a spot pattern match, which if found is confirmed visually by the user. If the shark is not matched the process is repeated and then the entire database is checked manually to ensure the individual is a new shark. This allows the MWSRP to determine which sharks regularly reside at SAMPA, as well as how many new sharks are visiting the area. Following the identification of each shark, encounter data and photos are uploaded to the Big Fish Network, an online portal with over 70 contributors. This allows contributors to see which whale sharks are within the MPA as well as at different atolls in the Maldives, whilst increasing the search effort and data collection of the MWSRP.

The MWSRP began year round data collection in 2014, hence the data utilised is the most comprehensive available. Search effort over this duration has been inconsistent due to periods of unfavourable weather and the SW monsoon. This monsoon brings rain and rough seas, disrupting surveying and concentrating the survey range predominately to the South and East of the MPA, from Dhigurah to Nalaguraidhoo (J. Hancock, pers.comm, Director MWSRP, 10 March 2017). Nevertheless, the data collected by the MWSRP represents one of the most consistent and detailed records of whale shark aggregations in the world.

To ensure accuracy, data was refined to include only encounter data and environmental data collected by the MWSRP team. An eight-day composite of chlorophyll a and sea surface temperature were downloaded from the SNPP-VIIRS instrument and the Aqua MODIS satellite at a 4km resolution (NASA 2017). From the available satellite data, this eight-day composite provided the most accurate coverage of the study site over the shortest time frame possible. A mean of whale sharks per day (shark encounters/search effort) and environmental variables were then calculated over the same time period to allow for accurate comparisons between data. Taking a mean of data also served to reduce the impact of any erroneous data collected (Moore, 1996). Lunar stage data was used from timeanddate.com, a source utilised in previous MWSRP publications and considered the most accurate available (Evans, 2012; Rees pers.comm, Director MWSRP, 2017). Data were combined from environmental data, encounter data and no shark data, providing the most detailed data collection of environmental variables possible.

2.3 Statistical Analysis

Statistical analyses were carried out using R (version 3.3.2; http://cran.r-project.org). The twelve predictor variables utilised were sea temperature (collected using a thermometer at SAMPA), wind direction, wind speed (Beaufort wind force scale), cloud cover, sea state, current direction, current strength, secchi disk visibility, monsoon season, lunar stage (new, first quarter, full, third quarter), chlorophyll a (chloro a) and sea surface temperature (from MODIS satellite data). The response variable was mean sharks per day. Prior to modelling, variables with strong skew were transformed, mean sharks (log+1) and chloro a (sqrt(sqrt)). As a mean of whale sharks per day is the response variable, a Gaussian Generalised Linear Model (GLM) was utilised. Variance testing was employed to highlight heteroscedasticity, of which none was found and all assumptions were met. None of the variables showed intercorrelation (maximum Pearson correlation -0.5), subsequently all variables were added to a single GLM to provide the maximum statistical power. By using backward-forward-stepwise-reduction a Minimum Adequate Model (MAM) was created, based on the Akaike Information Criterion (AIC). A univariate test was used to measure the significance of removed variables. All showed no significance to whale shark mean per day. The deviance of the MAM was analysed to ensure that the deviance observed was not reduced compared to the full GLM model. The probability values generated by the MAM were then compared with the False Discovery Rate (FDR) end point adjustment (Benjamini & Hochberg, 1995) to obtain an alpha value. This corrected the significance of p values, adjusting for type 1 errors arising due to repetitive testing. Finally, due to its importance to *R.typus* prey aggregations and its exclusion from the MAM, lunar stage was tested independently using an ANOVA.

2.4 GIS

Using ArcMap 10.4.1, a template of the South Ari Atoll MPA was created using known coordinates from SAMPA ((2017) appendices, figure 14). Points were edited to ensure they began at the reef edge and a 1km buffer was added, creating a shapefile of the MPA. The Imagerie Satellite layer was used as a base map due to its distinct display of the epipelagic reef fringe, from which the MPA extends. Using zonal statistics, the SAMPA shape file was used to spatially partition SST and chloro a values from each eight-day composite, from which a mean was calculated and used for statistical analysis.

Using GPS data recorded from each R.typus encounter as point data (n=1043), a kernel density plot of whale shark encounters was created over the study site to show species distribution and density.

Bathymetric data of the study site was downloaded from the General Bathymetric Chart of the Oceans (GEBCO) at a 1km, 30 arc-second interval global grid (GEBCO, 2015). This data was used for observational rather than analytical purposes.

3. Results

3.1 GIS results

The kernel density map below (figure 5) highlights the distribution of *R.typus* encounters (n=1043) over the study period. The density values show increased density of shark encounters along the epipelagic reef fringe, compared with the channels between islands, such as to the east of Maamigili (see figure 3 for island labels). Additionally, *R.typus* encounters display the highest density in the South of the MPA (red and orange). Also of importance is the density of shark encounters in the East of SAMPA, showing that sharks are distributed between two main areas within the MPA.

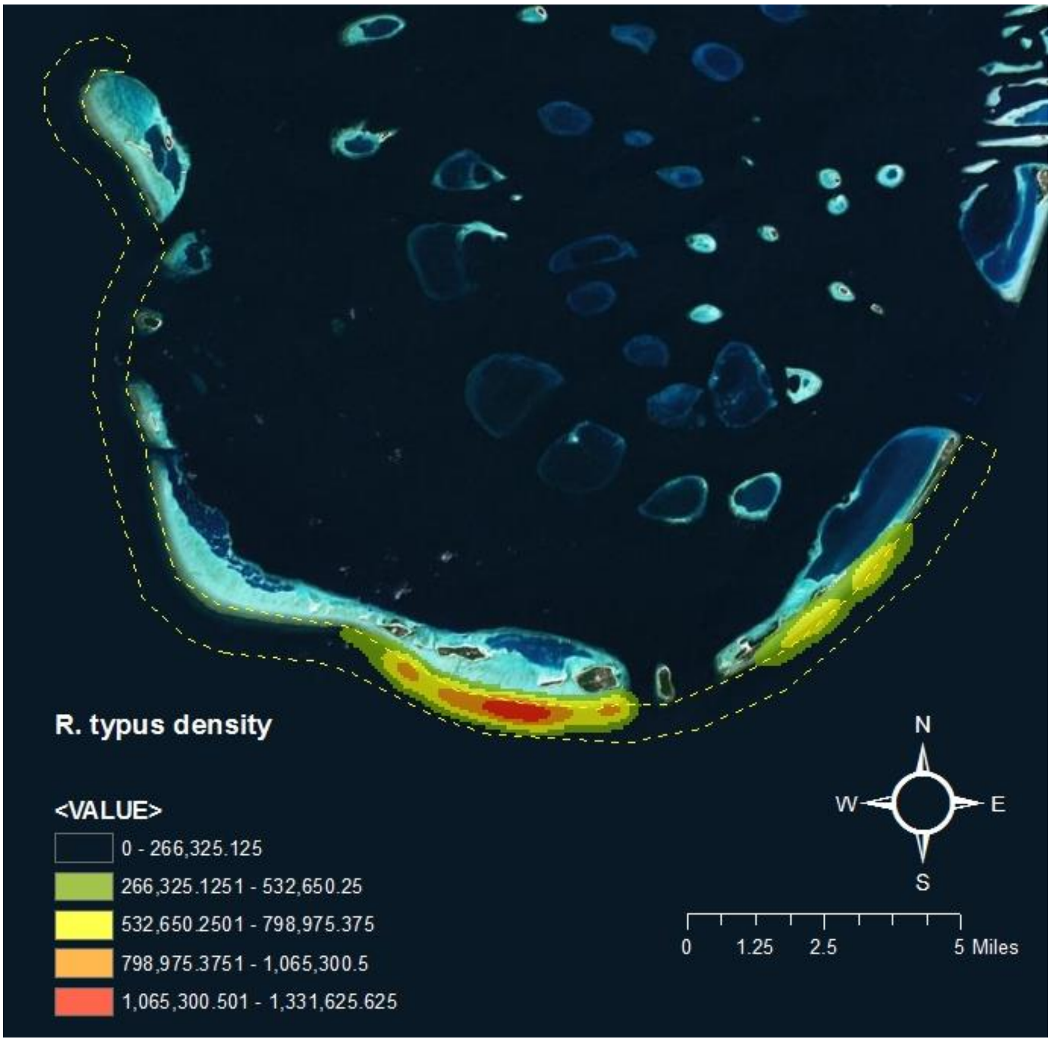

Figure 5: R.typus kernel density plot showing all whale shark encounters (n=1043) over the study period (1st January 2014 - 18th April 2017). The MPA (yellow dotted line) straddles the reef (pale blue) with islands (brown) and lagoons behind (mid blue).

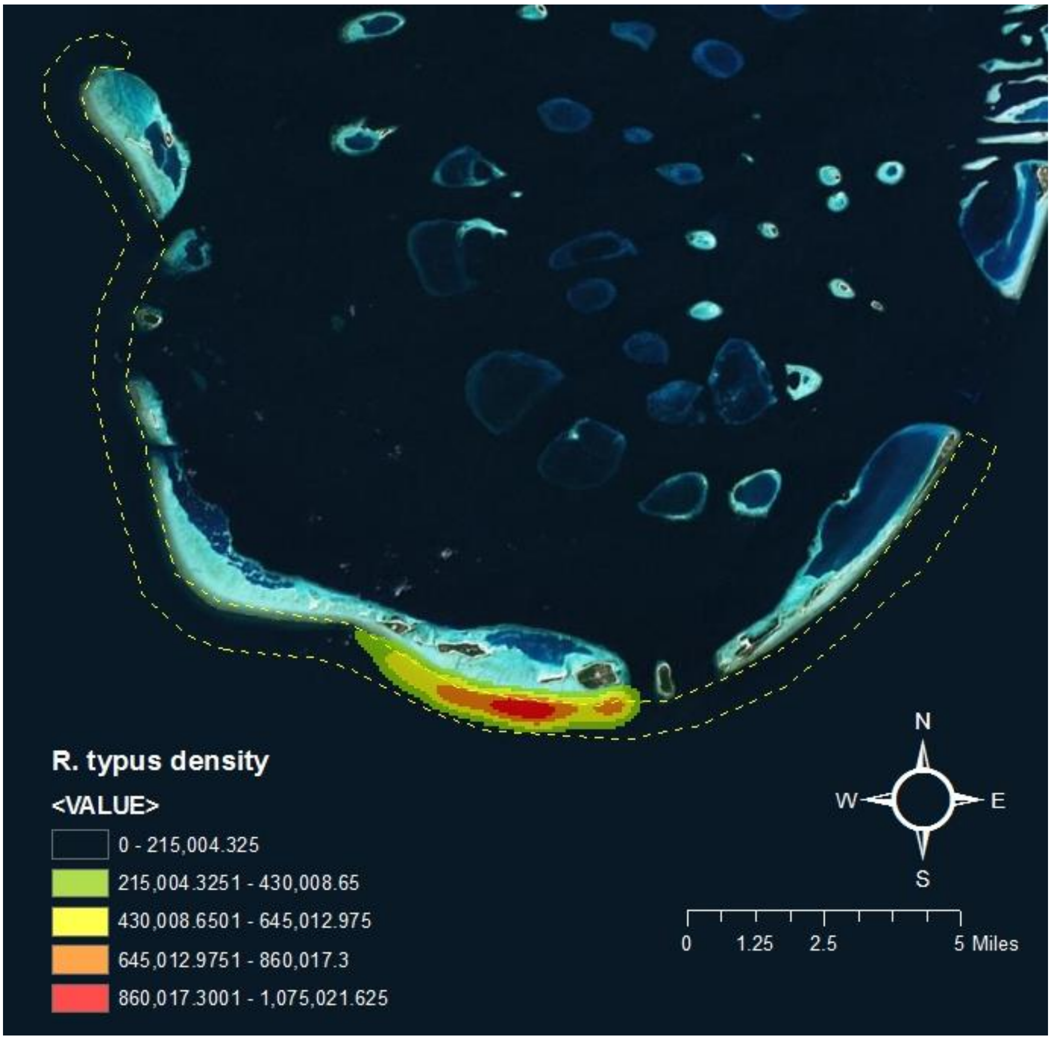

Figure 6: During the NE monsoon (November to April) whale shark encounter density is concentrated in the South of SAMPA, inferring that whale sharks aggregate predominately in this area (n=645).

When comparing the above density plot to figure 7 below, there is a noticeable shift in shark encounter density between the monsoon seasons. Density shifts dramatically from South to East, with sharks maintaining a presence in the South during the SW monsoon, but with considerably higher density to the East. The density of whale shark encounters is lower during the SW monsoon than the NE monsoon, showing a more general use of the MPA, compared with the concentrated density of encounters during the NE monsoon in the South.

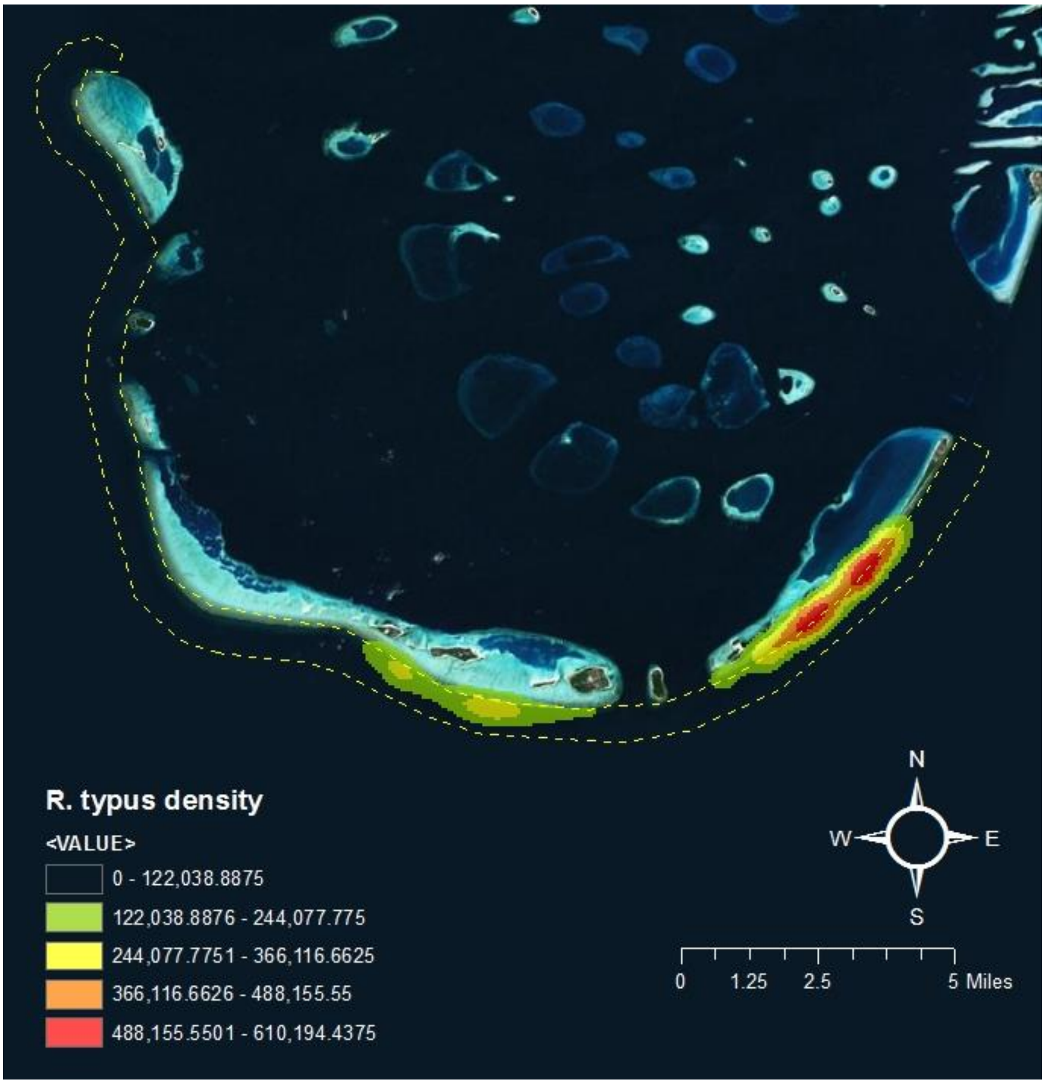

Figure 7: The SW monsoon shows a marked change in the distribution of R.typus encounter density (n=398) throughout the MPA when compared with the NE monsoon (figure 6). Note, the increased number of encounters in the NE monsoon are largely due to the study period finishing before the commencement of the 2017 SW monsoon.

3.2 Statistical Analysis

Table 1: Generalised linear model of mean whale sharks vs all environmental and biological predictor variables. MAM statistical results show the direction of the trend, positive (+) or negative (-), the % deviance explained and the probability of decreased deviance from the full model p[D]. Predictor variables were tested against the response variable (mean sharks per day, mean = 1.45, standard deviation (SD) ±0.59. Emboldened variables show those with the strongest significance after FDR correction (α = 0.026).

Model name (and variables tested)	Minimum Adequate Model
Full model (lunar stage, sea temperature, wind direction, wind speed, cloud cover, sea state, current direction, current strength, secchi disk visibility, chloro a, satellite sea surface temperature, monsoon season)	Sea temperature (+) p = 0.0626 %D = 2.44 Cloud cover (-) p = 0.2071 %D = 4.17 **Current strength** (-) p = 0.0058 %D = 4.81 **Chloro a** (+) p = 0.0217 %D = 4.81 Overall model: AIC = 165.85, p[D] = 0.8654, %D = 13.62

Table 1 shows that of all the predictor variables, the MAM selected current strength and chloro a as significant to the response variable (mean whale sharks per day), the P values of 0.0058 and 0.0217 confirm this. The percentage deviance (%D) shows that the significant variables explain a small percentage of the deviance in mean whale sharks per day. The MAM also selected temperature and cloud cover, however these were not significant. The results of the MAM are validated by the AIC score of 165.85 and p[D] = 0.8654, showing the MAM is of higher quality than the standard GLM (AIC 194.37) and that there is no significant difference between the GLM and MAM results.

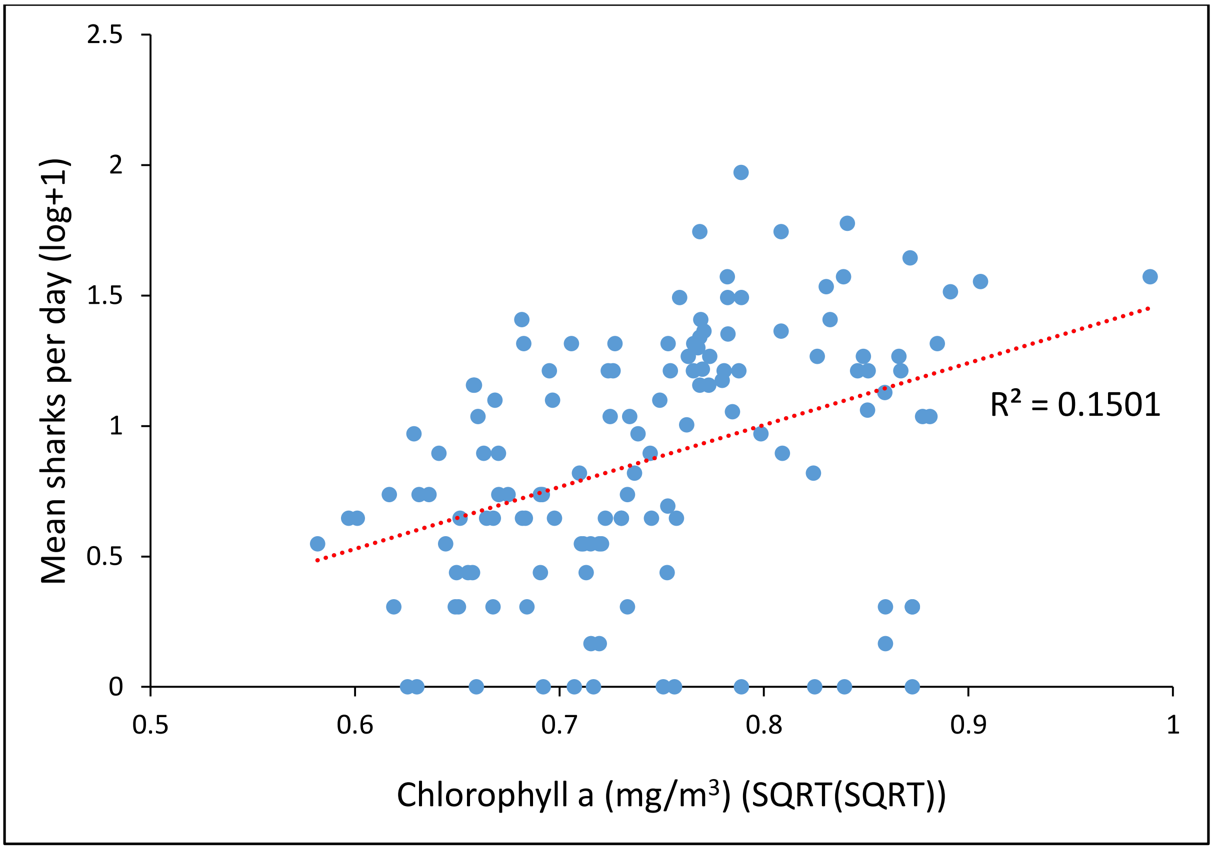

Figure 8: Scatterplot showing that the measure of chlorophyll a positively predicts mean sharks per day (P=0.0217). It also shows that high chlorophyll a concentrations do not always result in high mean sharks per day. The plot shows fluctuations between 0 and 1.97 mean sharks per day (log+1) despite matching chlorophyll a concentrations of 0.78 mg/m^3. Overall the plot displays a positive relationship between the variables, with the R^2 value of 0.1501 indicating high variability within the data, as shown by the spread of points.

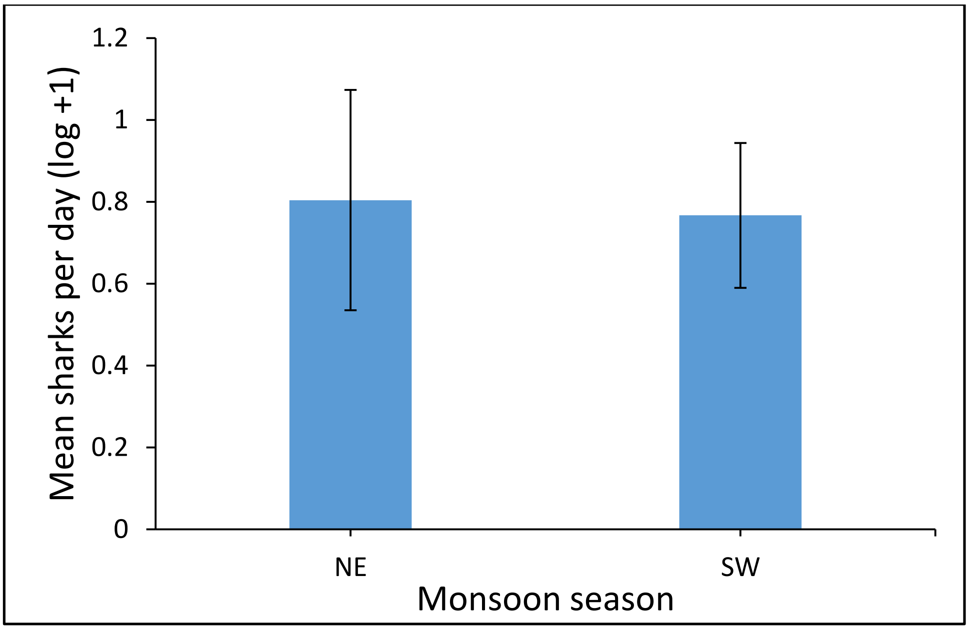

Figure 9: No significance was found between the NE and SW monsoon seasons and mean sharks per day. This graph illustrates the lack of significance between the variables. Standard Deviation (SD) NE monsoon ±0.27, SW Monsoon ±0.18.

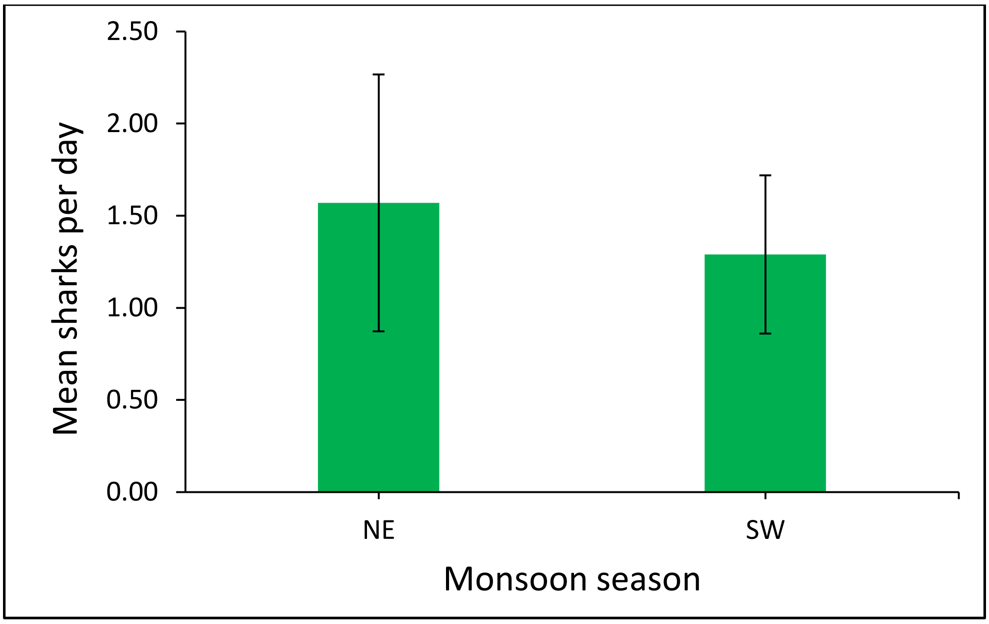

Figure 10: The mean number of sharks per day during the NE monsoon (1.57) was higher than during the SW monsoon (1.29). However, the standard deviation bars show the spread of mean sharks per day over the study period had larger deviation during the NE monsoon (SD NE monsoon ±0.70, SW Monsoon ±0.43).

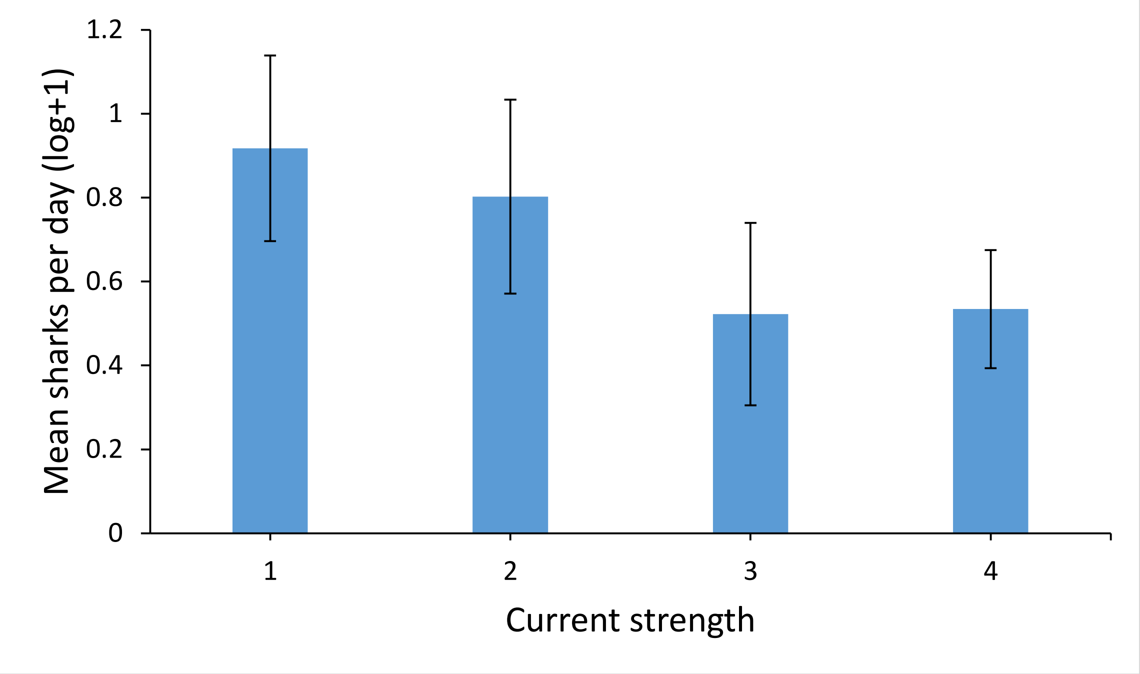

Figure 11: Current strength showed a significant (P=0.0058) negative relationship with mean sharks per day (log+1) with higher current speeds resulting in lower mean sharks per day. Also shown above is that the lowest current speed (1) had the highest mean sharks per day (log+1). A slight decrease is observed between current speeds 1 and 2 and mean sharks per day (log+1) with a substantial reduction in mean sharks per day (log+1) thereafter (SD 1 ±0.22, 2 ±0.23, 3 ±0.22, 4 ±0.14, Sample size 1 n=42, 2 n=59, 3 n=25, 4 n=5).

Table 2: ANOVA results from the analysis of Lunar stage with mean whale sharks per day. Each year was tested individually and then all years were tested together (Combined). The P values highlight the lack of significance between mean sharks per day and lunar phase. The low count of phases in 2017 is due to the study period ending on 18th April 2017.

Year	Phases	F Value	Significance level (P)
2014	n=37	F=0.507	P=0.680
2015	n=42	F=1.187	P=0.328
2016	n=38	F=1.022	P=0.395
2017	n=14	F=1.087	P=0.399
Combined	n=131	F=1.233	p=0.301

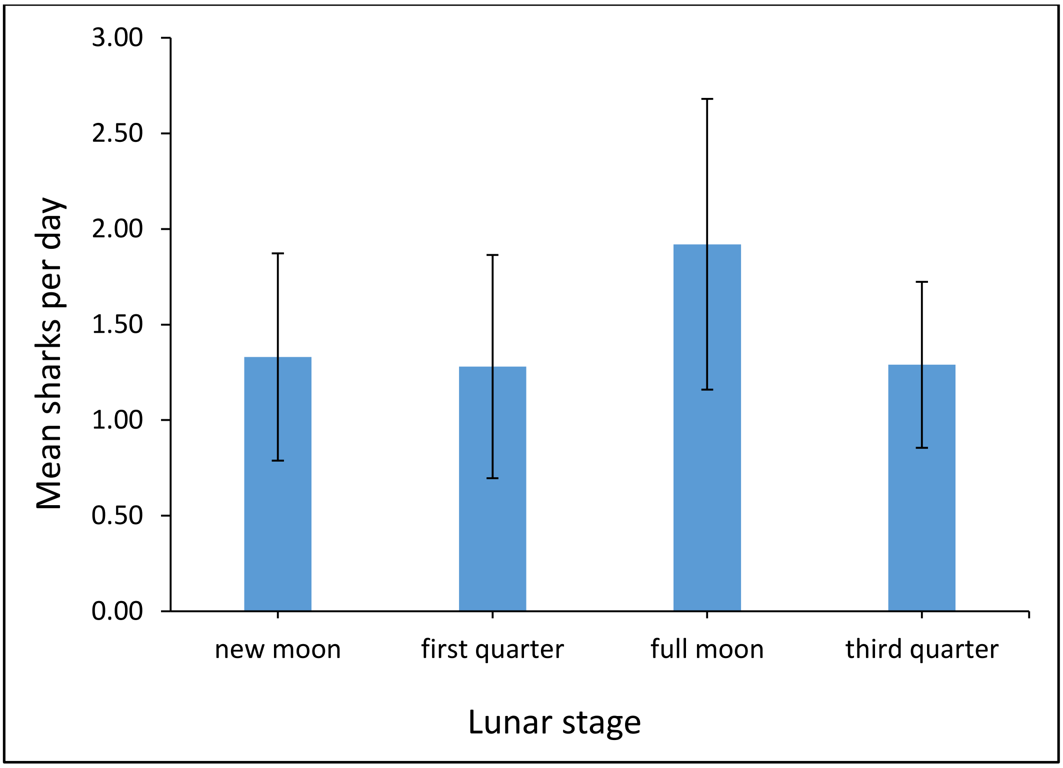

Figure 12: Mean R.typus per day per lunar stage 2014 – 2017. Although it can be seen that mean sharks is higher during the full moon stage, this was not significant (P=0.301, mean = 1.92). Apart from the full moon, all lunar stages showed similar mean sharks per day between 1.33 and 1.28. The standard deviation shows that within each lunar phase the number of sharks fluctuates greatly (SD new moon ±0.54, first quarter ±0.58, full moon ±0.76, third quarter ±0.43, sample size - new moon n=32, first quarter n=32, full moon n=34, third quarter n=32).

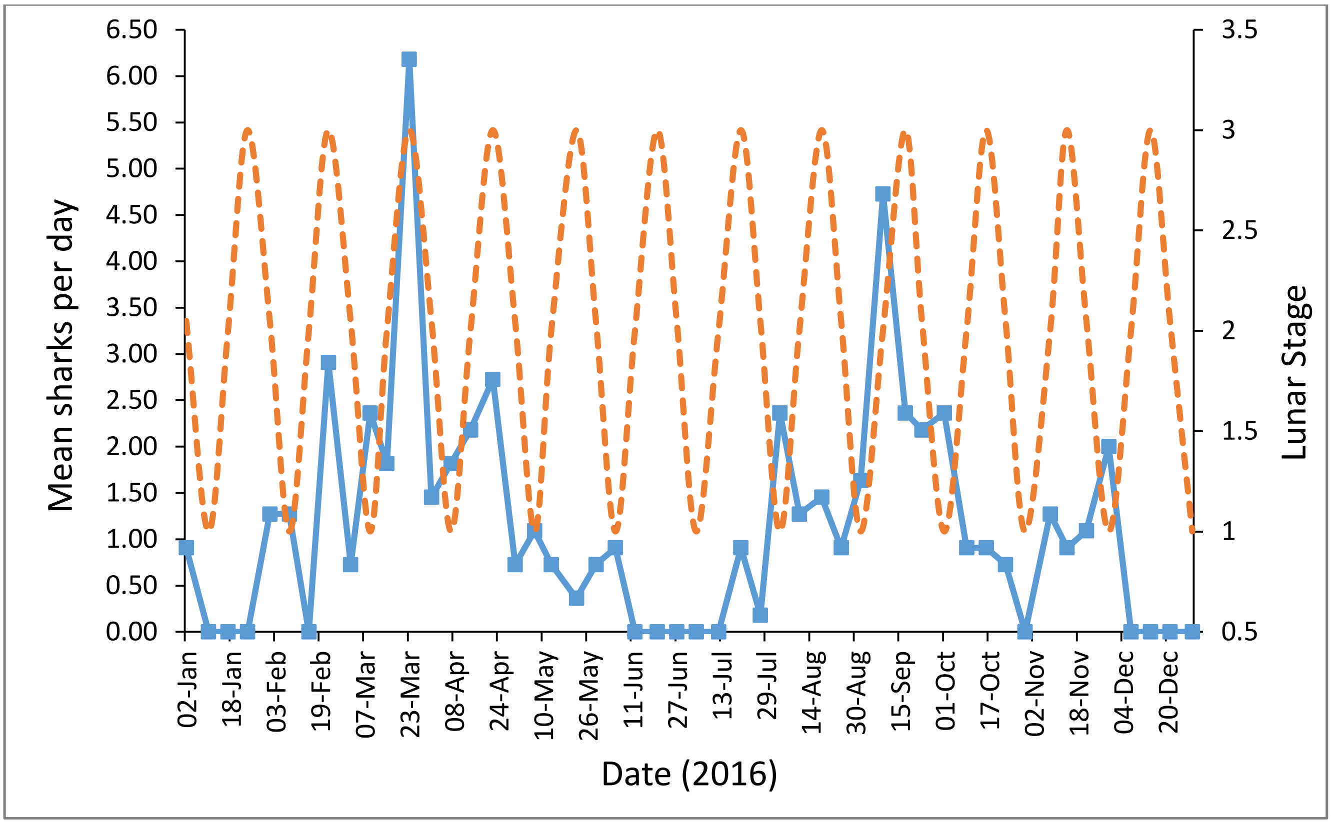

Figure 13: Mean whale sharks per day per lunar stage in 2016. Lunar stage 1 - new moon, 2 - first & third quarter, 3 - full moon. The ANOVA showed that lunar stage and mean sharks per day had no significant relationship. The high of mean sharks per day of 6.18 sharks during the March full moon is likely due to the mass spawning of acropora corals at SAMPA. The 0 mean sharks visible in June, July and December are due to a lack of search effort. The 0 mean sharks in February and November are 'shark droughts'.

4. Discussion

4.1 Summary

This study indicates that the most important environmental and biological variables to whale shark site fidelity at SAMPA are current strength, chlorophyll a concentration and temperature, as shown by the MAM. Of these variables, chlorophyll a (P=0.0217) and current strength (P=0.0058) were found to have a significant relationship (α=0.026).

Of all the variables, current strength showed the strongest relationship with mean sharks per day and the only significant negative relationship. Over the study period, a low current strength of 1 or 2 resulted in mean sharks of 1.73 and 1.48, whereas higher current strengths of 3 and 4 showed a marked, statistically significant reduction in mean sharks to 0.87 and 0.88 (appendices, figure 19). This may be in part due to the bathymetrically unrestricted habitat of South Ari Atoll which has depths in excess of 3000m within 15 miles of SAMPA (appendices, figure 15). Previous research has shown that *R.typus* conduct deep foraging dives in waters with temperatures as low as 3.4^{o}C (Brunnschweiler *et al*, 2009). Following these dives sharks are known to spend time recovering, using warmer surface waters for thermoregulation (Thums *et al*, 2012). The negative relationship may be due to the increased effort required to swim against currents when sharks are fatigued from energetically intensive vertical migrations (Sleeman *et al*, 2010b), with higher currents deterring sharks from surface waters. However, in other sites sharks have been observed opening their mouths into the current in order to encourage the flow of warm water over their gills, speeding up thermoregulation following vertical migrations (Wilson *et al*, 2006).

Whatever the cause of the relationship between current strength and mean sharks, inferring robust conclusions is difficult because unequal variance was observed between factor levels, therefore any significance must be treated with caution. Furthermore, current strength is estimated by MWSRP staff and volunteers based on their personal observations whilst swimming (1=low, 4=high). Consequently, a scientifically accurate, standardised measure needs to be developed to collect current data, allowing further research to ascertain the validity of any significant relationship.

Chlorophyll a showed a positive relationship with higher mean sharks per day observed during periods of higher chlorophyll a. *R.typus* prey such as zooplankton are associated with high chlorophyll a concentrations (Hsu *et al*, 2007; Sequeira *et al*, 2014; Lee *et al*, 2015) and whale sharks have been shown to reside for longer periods in areas with higher chlorophyll a content (Taylor & Pearce, 1999; Hsu *et al*, 2007; McKinnery *et al*, 2012; Afonso *et al,* 2014). The chlorophyll a data in this study is measured from a depth of 0-40m and hence is a measure of surface chlorophyll a concentrations (Sleeman *et al*, 2010b). This measurement range is important in that high chlorophyll a at this depth range may encourage whale sharks to reside in shallow surface waters due to their opportunistic feeding habits (Rowat & Gore, 2007; McKinney *et al*, 2012), thus increasing the likelihood of encounters.

Chlorophyll a levels are not consistent at SAMPA with large fluctuations observed throughout the study period (min = 0.12mg/m^3, max = 0.96 mg/m^3, mean = 0.31 mg/m^3). However, corresponding fluctuations are not always observed with mean whale sharks. In fact, throughout the data set there are numerous examples of high chlorophyll a concentration with 0 mean sharks per day. These irregularities, as well as its statistical significance, infer that chlorophyll a is at most a contributing factor, rather than a driver of whale shark site fidelity at SAMPA.

Sea temperature (collected in the field) was included in the MAM and existing research has shown SST to be an important driver of global whale shark aggregations and distributions (Rowat & Brooks, 2012, Sequiera *et al*, 2014). Although no doubt important, in this study temperature did not show a significant relationship with mean sharks per day (P = 0.0626). Sea temperature has been shown to have a close association with chlorophyll a (Sequiera *et al*, 2011), encouraging biological productivity and consequent whale shark prey aggregations (Hacohen-Domené *et al*, 2006) which may explain its inclusion in the MAM.

Although previous studies have analysed the environmental variables driving whale shark aggregations at SAMPA, this study has looked in more detail at chlorophyll a, lunar and SST records, as well as analysing the most comprehensive database of environmental variables to date. Furthermore, the data utilised covers a number of unusually high and low encounter periods. Five eight-day periods with an average of more than four sharks per day were analysed in this study, as well as a period from February 22nd to March 19th 2017 with zero encounters. These periods showed no discernible change in environmental variables, indicating that these are not the drivers of whale shark aggregations at SAMPA.

4.2 Limitations

Spotting whale sharks requires experience and a trained eye, but the high turnover of volunteers at MWSRP reduces the effectiveness of shark spotting at the beginning of each new volunteer intake. Rough seas and overcast weather further inhibit spotting sharks, as well as limiting search effort to calmer areas of the study site. Moreover, weather conditions are made more challenging by the SW monsoon, restricting search effort to the South and East. Consequently, the encounter data utilised in this study should be considered an underestimate of whale shark populations and density throughout SAMPA.

Search effort was not consistent over the study period with search effort records showing contradictions between days off and shark encounter days. Subsequently, search effort was based on a record of time in and out of the field. With a consistent record of search effort each day, a more precise measure of mean shark encounters per day could be calculated. Subsequently, mean sharks per day in this study is likely an underestimate.

Whale sharks are known to possess the largest inner ear in the animal kingdom, far larger than those of whales (Muller, 1999; Rowat & Brooks, 2012) and research at Ningaloo reef has shown that upon hearing the sound of tourist vessels, some sharks dive to deeper waters to avoid encounters (Martin, 2007; Sanzogni *et al*, 2015). The research vessel used by the MWSRP is relatively slow and noisy and may deter sharks, disturbing their thermoregulation and reducing the perceived density of whale sharks at SAMPA.

4.3 Conclusions

SAMPA provides favourable conditions for whale sharks, with warm sea surface temperatures, unrestricted bathymetry (appendices, figure 15) and peaks in prey abundance due to spawning fish and acropora corals (Loch *et al*, 2002). Furthermore, sharks showing wounds and scars from opportunistic bites from predators are seldom seen (pers.obs), whilst commonplace at neighbouring atolls (I. Shameel, pers.comm, Project Coordinator, Olive Ridley Project). As 86% of sharks observed at SAMPA are immature (Riley *et al*, 2010), these factors show SAMPA to be an attractive site for juvenile sharks, allowing them to feed and grow whilst avoiding predation.

The environmental and biological variables analysed affect the year round aggregation of whale sharks at SAMPA, but they are not the primary drivers of whale shark site fidelity. Although chlorophyll a may contribute to increased prey abundance, and was found to be significant in this study, it does not explain the consistent presence of whale sharks in the MPA. Anderson *et al* (2011) has shown that during the NE monsoon, currents flow towards the West of South Ari Atoll, causing upwelling, whereas during the SW monsoon currents flow East, causing upwelling towards the eastern side of the atoll. From the density maps created it appears sharks are following these nutrient rich upwellings and that they may act as a driver of whale shark aggregations at SAMPA. In order to confirm the factors affecting whale shark aggregations and distribution at SAMPA, new areas of data collection and further research are needed.

A tagging programme was initiated by the MWSRP in 2009, however it was met with strong criticism from the local community. If enough support could be garnered from local communities, the tagging of whale sharks would provide details of their horizontal and vertical movements around SAMPA (Wilson *et al*, 2006). Until this occurs, the growing database and popularity of the Big Fish Network (BFN) continues to provide a non-invasive, albeit less reliable, method of tracking whale sharks in the region. Another area of potential research could focus on the mesopelagic prey items of whale sharks, their abundance, vertical migrations, and potential as motivators of whale shark aggregations at SAMPA.

Ultimately, SAMPA urgently needs a management plan and regulation enforcement to ensure that its year round population of whale sharks are conserved for the future, allowing for the continued research of this intriguing population.

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References

Acuña-Marrero, D., Jiménez, J., Smith, F., Doherty Jr, P., Hearn, A., Green, J., Paredes-Jarrín, J., Salinas-de-León, P. 2014. Whale shark (Rhincodon typus) seasonal presence, residence time and habitat use at Darwin Island, Galapagos Marine Reserve. *PLoS One*, 9(12), p.e115946.

Afonso, P., McGinty, N., Machete, M. 2014. Dynamics of whale shark occurrence at their fringe oceanic habitat. *PLoS One*, 9(7), p.e102060.

Anderson, R, and Ahmed, H. 1993. *Shark Fisheries of the Maldives*. Rome: Ministry of Fisheries and Agriculture, Maldives, and FAO.

Anderson, R., Adam, M, and Goes, J. 2011. From monsoons to mantas: seasonal distribution of Manta alfredi in the Maldives. *Fisheries Oceanography*, 20(2), 104 - 113.

Balch, W, and Byrne, C. 1994. Factors affecting the estimate of primary production from space. *J Geophys Res* 99: 7555–7570.

Barbosa-Filho, M., Tavares, D., Siciliano, S., de Moura, J., Costa-Neto, E., dos Santos Motta, F., Koike, C. 2016. Interactions between whale sharks, *Rhincodon typus* (Smith, 1928, *Orectolobiformes, Rhincodontidae*), and Brazilian fisheries: The need for effective conservation measures. *Marine Policy*, 73, pp.210-215.

Benjamini, Y, and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the royal statistical society*. Series B (Methodological), pp.289-300.

Berumen, M., Braun, C., Cochran, J., Skomal, G., Thorrold, S. 2014. Movement patterns of juvenile whale sharks tagged at an aggregation site in the Red Sea. *PLoS One*, 9(7), p.e103536.

Brunnschweiler, J., Baensch, H., Pierce, S., and Sims, D. 2009. Deep-diving behaviour of a whale shark Rhincodon typus during long-distance movement in the western Indian Ocean. *Journal of fish biology*, 74(3), pp.706-714.

Brunnschweiler, J, and Sims, D. 2011. Diel Oscillations in Whale Shark Vertical Movements Associated with Meso- and Bathypelagic Diving. *American Fisheries Society Symposium*, 76, pp.457-469.

Cagua, E., Collins, N., Hancock, J., and Rees, R. 2014. Whale shark economics: a valuation of wildlife tourism in South Ari Atoll, Maldives. *PeerJ* 2:e515; DOI10.7717/peerj.515.

Cagua, E., Cochran, J., Rohner, C., Prebble, C., Sinclair-Taylor, T., Pierce, S., Berumen, M. 2015. Acoustic telemetry reveals cryptic residency of whale sharks. *Biology letters*, 11(4), p.20150092.

Cardenas-Palomo, N., Herrera-Silveira, J., Reyes, O. 2010. Spatial and temporal distribution of physicochemical features in the habitat of whale shark *Rhincodon typus* (*Orectolobiformes: Rhincodontidae*) in the north of Mexican Caribbean. *Revista de biología tropical*, 58(1), pp.399-412.

Casey, J., Connett, S., Compagno, J., Stevens, J., Oulton, G., Cook, S. 1992. The status of pelagic elasmobranchs: concerns and commentary. *Chondros* 3, 3–6.

Castro, A., Stewart, B., Wilson, S., Hueter, R., Meekan, M., Motta, P., Bowen, B., Karl, S. 2007. Population genetic structure of Earth's largest fish, the whale shark (Rhincodon typus). *Molecular Ecology*, 16(24), pp.5183-5192.

Chen, C., Liu, K., Joung, S. 1997. Preliminary report on Taiwan's whale shark fishery. *Traffic Bulletin* 17, 53–57.

Chen, V., and Phipps, M. 2002. Management and trade of whale sharks in Taiwan. *Taipei TRAFFIC East Asia Report*.

Clarke, S. 2004. Understanding pressures on fishery resources through trade statistics: a pilot study of four products in the Chinese dried seafood market. *Fish and Fisheries*, 5(1), pp.53-74.

Colman, J. 1997. A review of the biology and ecology of the whale shark. *Journal of Fish Biology* 51, 1219–1234.

Compagno, L. 1984. Sharks of the world. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis No. 124, Vol. 4, FAO Rome (1984) Part 1.

Compagno, L. 2001. Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date, Vol.2. Rome: FAO.

de la Parra Venegas, R., Hueter, R., Cano, J., Tyminski, J., Remolina, J., Maslanka, M., Ormos, A., Weigt, L., Carlson, B. and Dove, A. 2011. An unprecedented aggregation of whale sharks, Rhincodon typus, in Mexican coastal waters of the Caribbean Sea. *PloS one*, 6(4), p.e18994.

Donati, G., Rees, R., Hancock, J., Jenkins, T., Shameel, I., Hindle, K., Zareer, I., Childs, A., Cagua, E. 2016. New insights into the South Ari atoll whale shark, *Rhincodon typus*, aggregation. *QScience Proceedings*, p.16.

Duffy, C. 2002. Distribution, seasonality, lengths, and feeding behaviour of whale sharks (Rhincodon typus) observed in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research*, 36 (3), pp.565-570.

Ebert, D., Mollet, H., Baldridge, A., Thomas, T., Forney, K., Ripley, W. 2004. Occurrence of the Whale Shark, Rhincodon typus Smith 1828, in California Waters. *Northwestern Naturalist*, 85(1), pp.26-28.

Eckert, S, and Stewart, B. 2001. Telemetry and satellite tracking of whale sharks, Rhincodon typus, in the Sea of Cortez, Mexico, and the North Pacific Ocean. *Environmental Biology of Fishes* 60: 299–308.

Eckert, S., Dolar, L., Kooyman, G., Perrin, W., Rahman, R. 2002. Movements of whale sharks (Rhincodon typus) in South-east Asian waters as determined by satellite telemetry. *Journal of Zoology*, 257(1), pp.111-115.

Evans, N. 2012. Analysis of observed tide data at Dhigurah in relation to predicted tide data at Male. Maldives Whale Shark Research Programme. Doc ref: 12345678. Accessed on 20/08/2017, < https://maldivesconservationportal.org/wp-content/uploads/2014/06/Analysis-of-Observed-Tide-Data-at-Dhigurah-in-Relation-to-Predicted-Tide-Data-at-Mal%C3%A9.pdf >

GEBCO, 2015. The GEBCO_2014 Grid, version 20150318. Accessed on 24/08/2017, <http://www.gebco.net >

Gifford, A., Compagno, L., Levine, M., Antoniou, A. 2007. Satellite tracking of whale sharks using tethered tags. *Fisheries Research* 84, 17–24.

Graham, R, and Roberts, C. 2007. Assessing the size, growth rate and structure of a seasonal population of whale sharks (Rhincodon typus Smith 1828) using conventional tagging and photo identification. *Fisheries Research*, 84(1), pp.71-80.

Graham, R., Roberts, C., and Smart, J. 2006. Diving behaviour of whale sharks in relation to a predictable food pulse. *Journal of the Royal Society Interface*, 3(6), pp.109-116.

Gunn, J., Stevens, J., Davis, T., Norman, B. 1999. Observations on the short-term movements and behaviour of whale sharks (Rhincodon typus) at Ningaloo Reef, Western Australia. *Marine Biology*, 135(3), pp.553-559.

Hacohen-Domené, A., Galvan-Magaña, F, and Ketchum-Mejia, J. 2006. Abundance of whale shark (Rhincodon typus) preferred prey species in the southern Gulf of California, Mexico. *Cybium*, 30(4), pp.99-102.

Hacohen-Domené, A., Martínez-Rincón, R., Galván-Magaña, F., Cárdenas-Palomo, N., de la Parra-Venegas, R., Galván-Pastoriza, B., Dove, A. 2015. Habitat suitability and environmental factors affecting whale shark (Rhincodon typus) aggregations in the Mexican Caribbean. *Environmental Biology of fishes*, 98(8), pp.1953-1964.

Hancock, J. 2017. Personal communication, *In: Mundy, E. Unpublished. Seasonal hotspots of mega-fauna and vessel activity in South Ari Marine Protected Area, the Maldives. MSc thesis, Environmental Marine Management, the University of York.*

Hausfather, Z. 2004. India’s shark trade: an analysis of Indian shark landings based on shark fin exports. *Marine Studies* (MAST) 3, 25–40.

Hearn, A., Espinoza, E., Green, J., Acuña-Marrero, D., Ryan, J. 2016. Association of adult female whale sharks with open ocean and coastal upwelling frontal systems in the Eastern Tropical Pacific. *QScience Proceedings*, p.24.

Heyman, W., Graham, R., Kjerfve, B., Johannes, R. 2001. Whale sharks Rhincodon typus aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* 215: 275–282.

Hobbs, J., Frisch, A., Hamanaka, T., McDonald, C., Gilligan, J., Neilson, J. 2009. Seasonal aggregation of juvenile whale sharks (Rhincodon typus) at Christmas Island, Indian Ocean. *Coral Reefs*, 28(3), pp.577-577.

Hoffmayer, E., Franks, J, and Shelley, J. 2005. Recent observations of the whale shark (Rhincodon typus) in the northcentral Gulf of Mexico. *Gulf and Caribbean Research*, 17(1), pp.117-120.

Hoffmayer, E., Franks, J., Driggers, W., Oswald, K., Quattro, J. 2007. Observations of a feeding aggregation of whale sharks, *Rhincodon typus*, in the north central Gulf of Mexico. *Gulf Carib Res* 19(2): 69–73.

Hsu, H., Joung, S., Liao, Y, and Liu, K. 2007. Satellite tracking of juvenile whale sharks, Rhincodon typus, in the Northwestern Pacific. *Fisheries Research*, 84(1), pp.25-31.

Irvine, T, and Keesing, J. 2007. Whale sharks: science, conservation and management. In: Proceedings of the First International Whale Shark Conference. *Fisheries Research,* 84.

IUCN Shark Specialist Group. 2016. Rhincodon typus, The IUCN Red List of Threatened Species. Version 2017-1. Spatial data downloaded on 14/08/2017, < http://www.iucnredlist.org >

Last, P, and Stevens, J. 1994. Sharks and rays of Australia. Australia: CSIRO.

Last, P, and Stevens, J. 2009. Sharks and Rays of Australia, 2nd edn. Collingwood: CSIRO.

Lee, Y., Matrai, P., Friedrichs, M., Saba, V., Antoine, D., Ardyna, M., Asanuma, I., Babin, M., Bélanger, S., Benoît-Gagné, M., Devred, E. 2015. An assessment of phytoplankton primary productivity in the Arctic Ocean from satellite ocean color/in situ chlorophyll-a based models. *Journal of Geophysical Research: Oceans*, 120(9), pp.6508-6541.

Lévy, M., Shankar, D., André, J., Shenoi, S., Durand, F., de Boyer Montégut, C. 2007. Basin-wide seasonal evolution of the Indian Ocean's phytoplankton blooms. *Journal of Geophysical Research*: Oceans, 112(C12).

Loch, K., Loch, W., Schuhmacher, H., See, W. 2002. Coral Recruitment and Regeneration on a Maldivian Reef 21 Months after the Coral Bleaching Event of 1998. *Marine Ecology*, 23(3), pp. 219–236.

Macena, B, and Hazin, F. 2016. Whale Shark (Rhincodon typus) seasonal occurrence, abundance and demographic structure in the Mid-Equatorial Atlantic Ocean. *PloS one*, 11(10), p.e0164440.

Martin, R. 2007. A review of behavioural ecology of whale sharks (Rhincodon typus). *Fisheries Research*, 84(1), pp.10-16.

McKinney, J., Hoffmayer, E., Wu, W., Fulford, R., Hendon, J. 2012. Feeding habitat of the whale shark Rhincodon typus in the northern Gulf of Mexico determined using species distribution modelling. *Marine Ecology Progress Series*, 458, pp.199-211.

Meekan, M., Bradshaw, C., Press, M., McLean, C., Richards, A., Quasnichka, S., Taylor, J. 2006. Population size and structure of whale sharks Rhincodon typus at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series*, 319, pp.275-285.

Moore, L.M., 1996. The basic practice of statistics. *Technometrics*, 38 (4), pp.404 -410.

Morgan, K, and Kench, P. 2016. Reef to island sediment connections on a Maldivian carbonate platform: using benthic ecology and biosedimentary depositional facies to examine island-building potential. *Earth Surface Processes and Landforms*, 41, 1815 – 1825.

Muller, M. 1999. Size limitations in semicircular duct systems. *Journal of Theoretical Biology* 198, 405–437. DOI: 10.1006/jtbi.1999.0922

Norman, B. 2004. Review of the current conservation concerns for the whale shark (*Rhincodon typus*): a regional perspective. Coast and Clean Seas Project 2127 Final Report to the Australian Government. Department of the Environment and Heritage, Canberra, Australia.

Pierce, S, and Norman, B. 2016. Rhincodon typus. The IUCN Red List of Threatened Species 2016: e.T19488A2365291. Accessed on 07/08/2017, < http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T19488A2365291.en >

Ramírez-Macías, D., Meekan, M., La Parra-Venegas, D., Remolina-Suárez, F., Trigo-Mendoza, M. and Vázquez-Juárez, R. 2012. Patterns in composition, abundance and scarring of whale sharks Rhincodon typus near Holbox Island, Mexico. *Journal of fish biology*, 80(5), pp.1401-1416.

Rasheed, A., Abdulla, A, and Zakariyya, N. 2016. Vulnerability of different types of fishers to potential implementation of a management plan in a Marine Protected Area (MPA) in the Maldives. *Marine Policy*, 74, 195-204

Raymont, J. 2014. Plankton & Productivity in the Oceans: Volume 1: Phytoplankton. Elsevier.

Rees, R. 2017. Personal communication. Director of Maldives Whale Shark Research Programme.

Reyes, O. 2009. Scientists discover the largest assembly of whale sharks ever recorded. Smithsonian Insider. Accessed on 11/08/2017, < http://insider.si.edu/2011/05/scientists-discover-the-largest-assembly-of-whale-sharks-ever-recorded/ >

Riley, M., Hale, M., Harman, A., Rees, R. 2010. Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives Archipelago. *Aquatic Biology* 8, 145–150.

Robinson, D., Jaidah, M., Jabado, R., Lee-Brooks, K., El-Din, N., Malki, A., Elmeer, K., McCormick, P., Henderson, A., Pierce, S., Ormond, R. 2013. Whale sharks, Rhincodon typus, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. *PLoS One*, 8(3), p.e58255.

Rohner, C., Pierce, S., Marshall, A., Weeks, S., Bennett, M., Richardson, A. 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.

Rowat, D, and Gore, M. 2007. Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. *Fisheries Research*, 84(1), pp.32-40.

Rowat, D., Brooks, K., March, A., McCarten, C., Jouannet, D., Riley, L., Jeffreys, G., Perri, M., Vely, M. and Pardigon, B. 2011. Long-term membership of whale sharks (Rhincodon typus) in coastal aggregations in Seychelles and Djibouti. *Marine and Freshwater Research*, 62(6), pp.621-627.

Rowat, D, and Brooks, K. 2012. A review of the biology, fisheries and conservation of the whale shark *Rhincodon typus*. *J Fish Biol* 80: 1019–1056.

Rowat, D., Meekan, M., Engelhardt, U., Pardigon, B., Vely, M. 2007. Aggregations of juvenile whale sharks (Rhincodon typus) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes*, 80(4), pp.465-472.

SAMPA. 2017. SAMPA Maldives, South Ari MPA. Accessed on 14/08/2017, < https://sampamaldives.wordpress.com/about-south-ari-marine-protected-area/ >

Sanzogni, R., Meekan, M., and Meeuwig, J. 2015. Multi-year impacts of ecotourism on whale shark (Rhincodon typus) visitation at Ningaloo Reef, Western Australia. *PloS one*, 10(9), p.e0127345.

Schmidt, J., Schmidt, C., Ozer, F., Ernst, R., Feldheim, K., Ashley, M., Levine, M. 2009. Low genetic differentiation across three major ocean populations of the whale shark, Rhincodon typus. *PloS one*, 4(4), p.e4988.

Sequeira, A., Mellin, C., Fordham, D., Meekan, M., Bradshaw, C. 2014. Predicting current and future global distributions of whale sharks. *Global change biology*, 20(3), pp.778-789.

Sequeira, A., Mellin, C., Rowat, D., Meekan, M., Bradshaw, C. 2012. Ocean-scale prediction of whale shark distribution. *Diversity Distrib* 18: 504–518.

Sequeira, A., Mellin, C., Meekan, M., Sims, D., Bradshaw, C. 2013. Inferred global connectivity of whale shark Rhincodon typus populations. *Journal of Fish Biology*, 82(2), pp.367-389.

Sleeman, J., Meekan, M., Fitzpatrick, B., Steinberg, C., Ancel, R., Bradshaw, C. 2010a. Oceanographic and atmospheric phenomena influence the abundance of whale sharks at Ningaloo Reef, Western Australia. *Journal of Experimental Marine Biology and Ecology*, 382(2), pp.77-81.

Sleeman, J., Meekan, M., Wilson, S., Polovina, J., Stevens, J., Boggs, G., Bradshaw, C. 2010b. To go or not to go with the flow: Environmental influences on whale shark movement patterns. *Journal of Experimental Marine Biology and Ecology*, 390(2), pp.84-98.

Stewart, B, and Wilson, S. 2005. Threatened fishes of the world: Rhincodon typus (Smith 1828) (Rhincodontidae). *Environ Biol Fishes* 74:184–185.

Taylor J. 1996. Seasonal occurrence, distribution and movements of the whale shark, Rhincodon typus, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* 47, 637-642.

Taylor, J, and Pearce, A. 1999. Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. *Journal of the Royal Society of Western Australia*, 82(2), pp.57-65.

Taylor, J. 2007. Ram filter-feeding and nocturnal feeding of whale sharks (Rhincodon typus) at Ningaloo Reef, Western Australia. *Fisheries Research*, 84(1), pp.65-70.

Thums, M., Meekan, M., Stevens, J., Wilson, S., Polovina, J. 2012. Evidence for behavioural thermoregulation by the world's largest fish. *Journal of The Royal Society Interface*, p.rsif20120477.

Tomita, T., Kawai, T., Matsubara, H., Kobayashi, M., Katakura, S. 2014. Northernmost record of a whale shark Rhincodon typus from the Sea of Okhotsk. *Journal of fish biology*, 84(1), pp.243-246.

Turnbull, S, and Randell, J. 2006. Rare occurrence of a Rhincodon typus (whale shark) in the Bay of Fundy, Canada. *Northeastern Naturalist* 13, 57–58.

Tyminski, J., de la Parra-Venegas, R., Cano, J., Hueter, R. 2015. Vertical movements and patterns in diving behavior of whale sharks as revealed by pop-up satellite tags in the eastern Gulf of Mexico. *PloS one*, 10(11), p.e0142156.

Vignaud, T., Maynard, J., Leblois, R., Meekan, M., Vázquez-Juárez, R., Ramírez-Macías, D., Pierce, S., Rowat, D., Berumen, M., Beeravolu, C., Baksay, S. 2014. Genetic structure of populations of whale sharks among ocean basins and evidence for their historic rise and recent decline. *Molecular ecology*, 23(10), pp.2590-2601.

Wilson, S., Taylor, J, and Pearce, A. 2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/Southern Oscillation. *Environmental Biology of Fishes*, 61(1), pp.1-11.

Wilson, S., Polovina, J., Stewart, B., Meekan, M. 2006. Movements of whale sharks (Rhincodon typus) tagged at Ningaloo Reef, Western Australia. *Marine Biology*, 148(5), pp.1157-1166.

Wolfson, F. 1986. Occurrences of the whale shark, *Rincodon typus* Smith. pp. 208–226. In: T. Uyeno, R. Aria, T. Taniuchi and K. Matsuura (ed.) Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes, Ichthyological Society of Japan, Tokyo.

NASA. 2017. Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Sea Surface Temperature Data; NASA OB.DAAC, Greenbelt, MD, USA. Accessed on 25/08/2017

Appendices

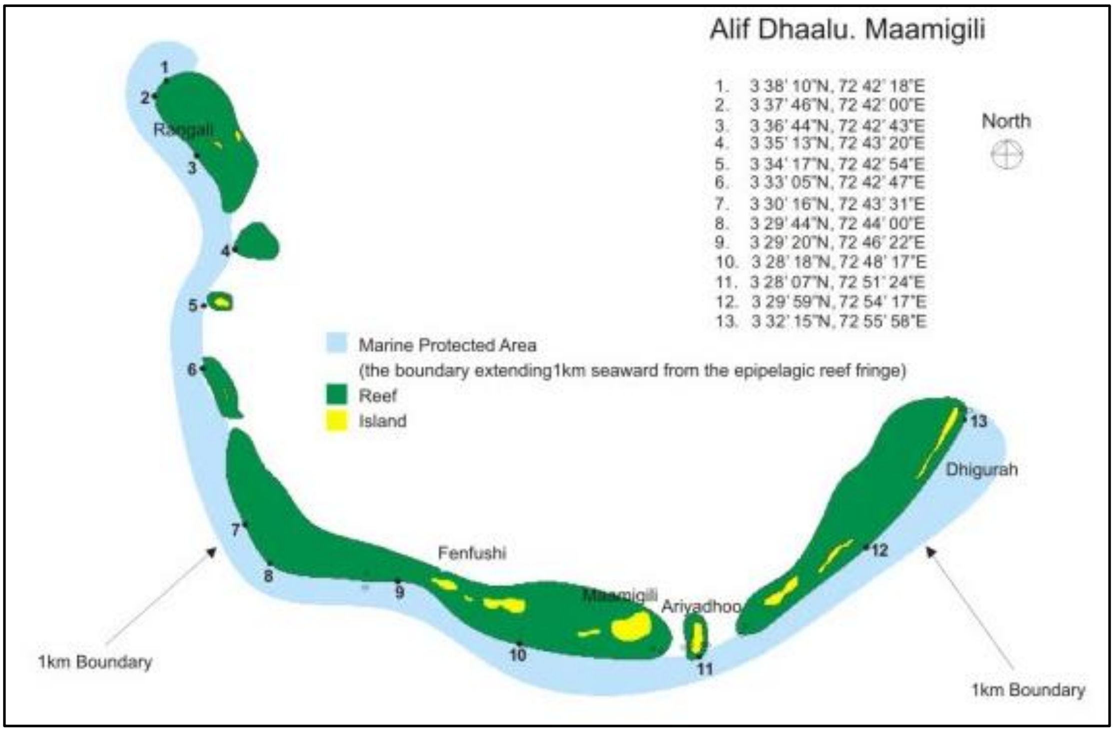


Figure 14: Map of SAMPA with detailed coordinates from which the MPA template was created using GIS (SAMPA, 2017).

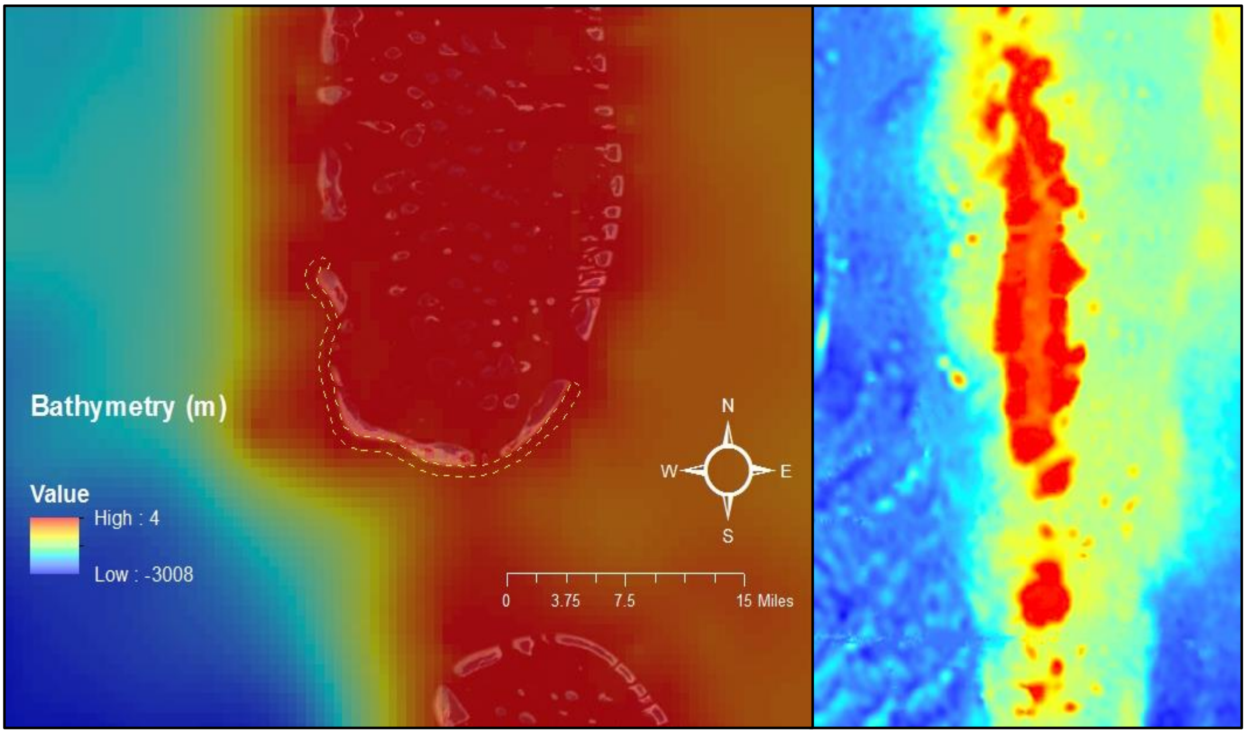


Figure 15: Bathymetry of the South Ari Atoll region

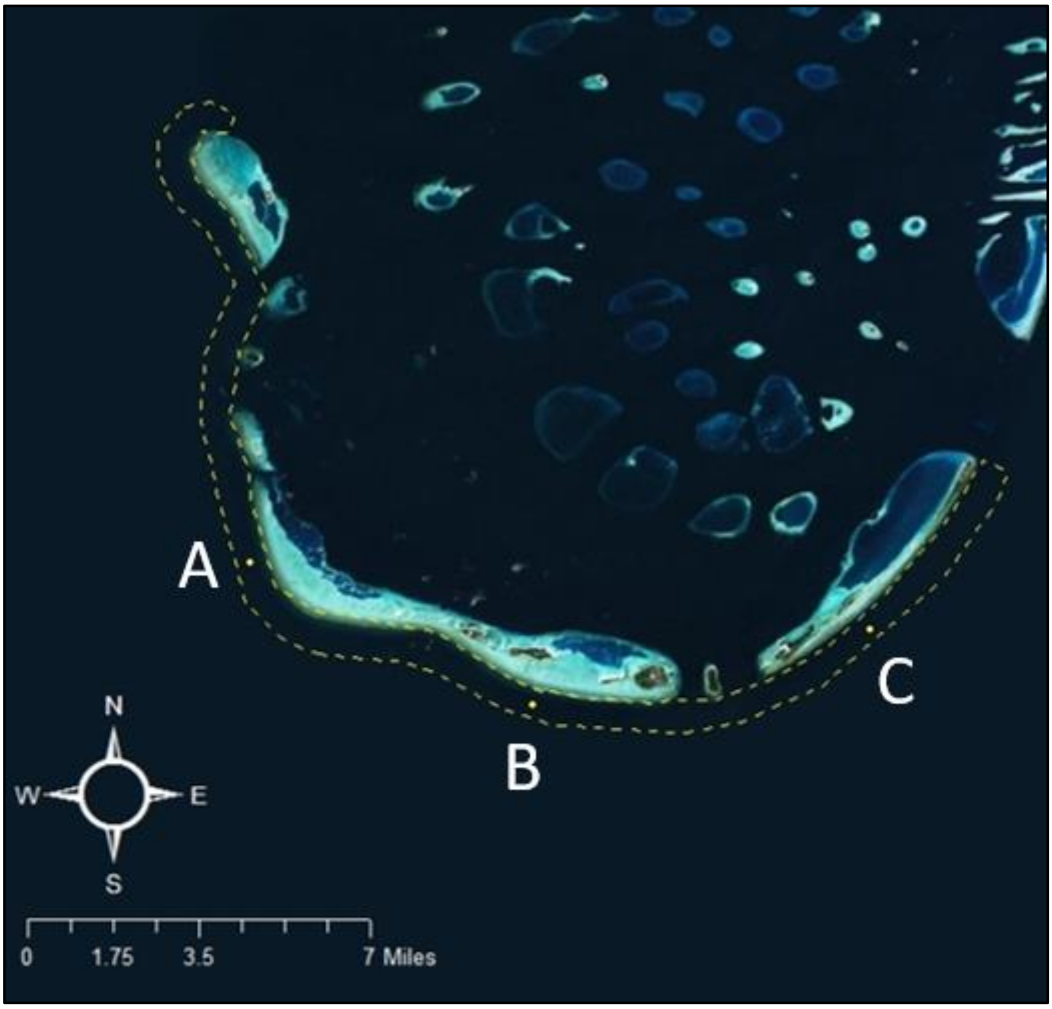


Figure 16: Typical position of environmental stations A, B and C. GPS locations where environmental variables are recorded daily, weather permitting, in addition to those recorded during shark encounters. The environmental data collected at the above sites were used to determine environmental and biological conditions present during days with no R. typus encounters.

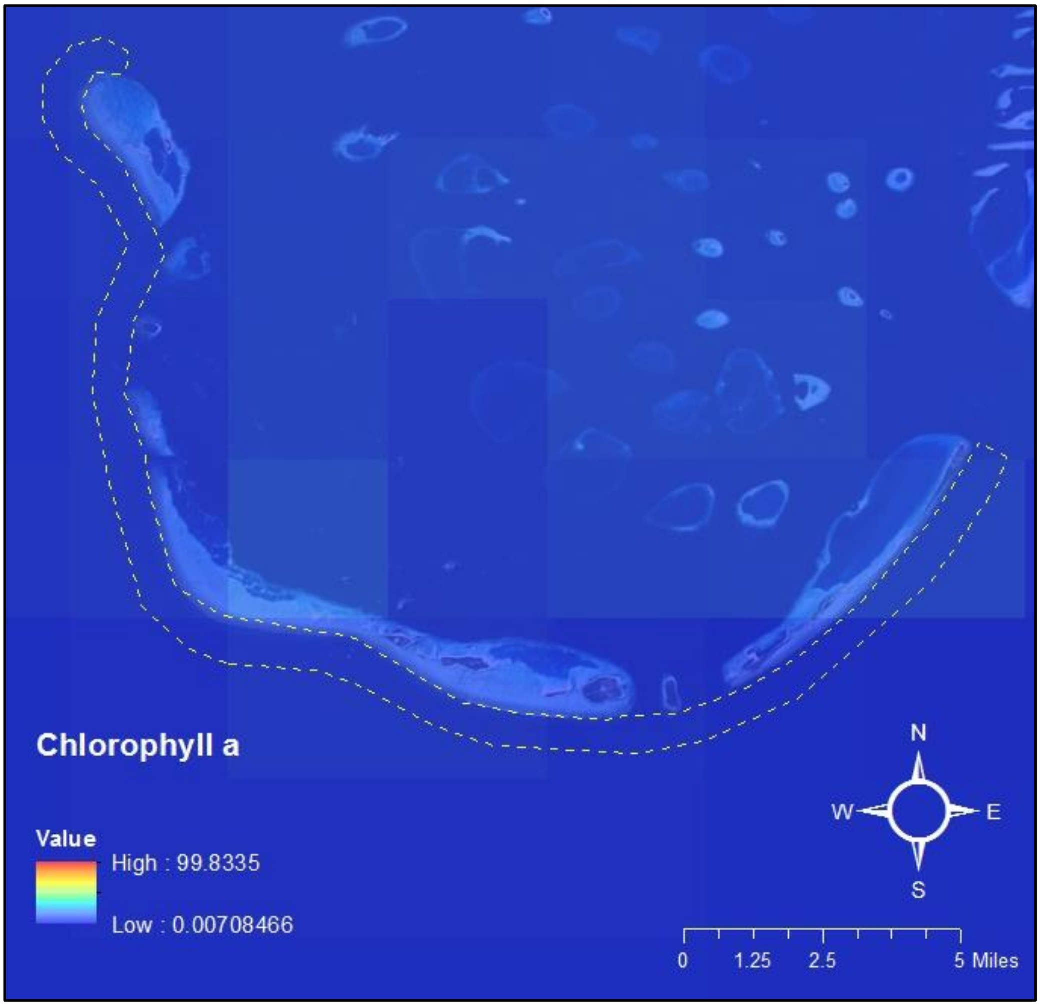
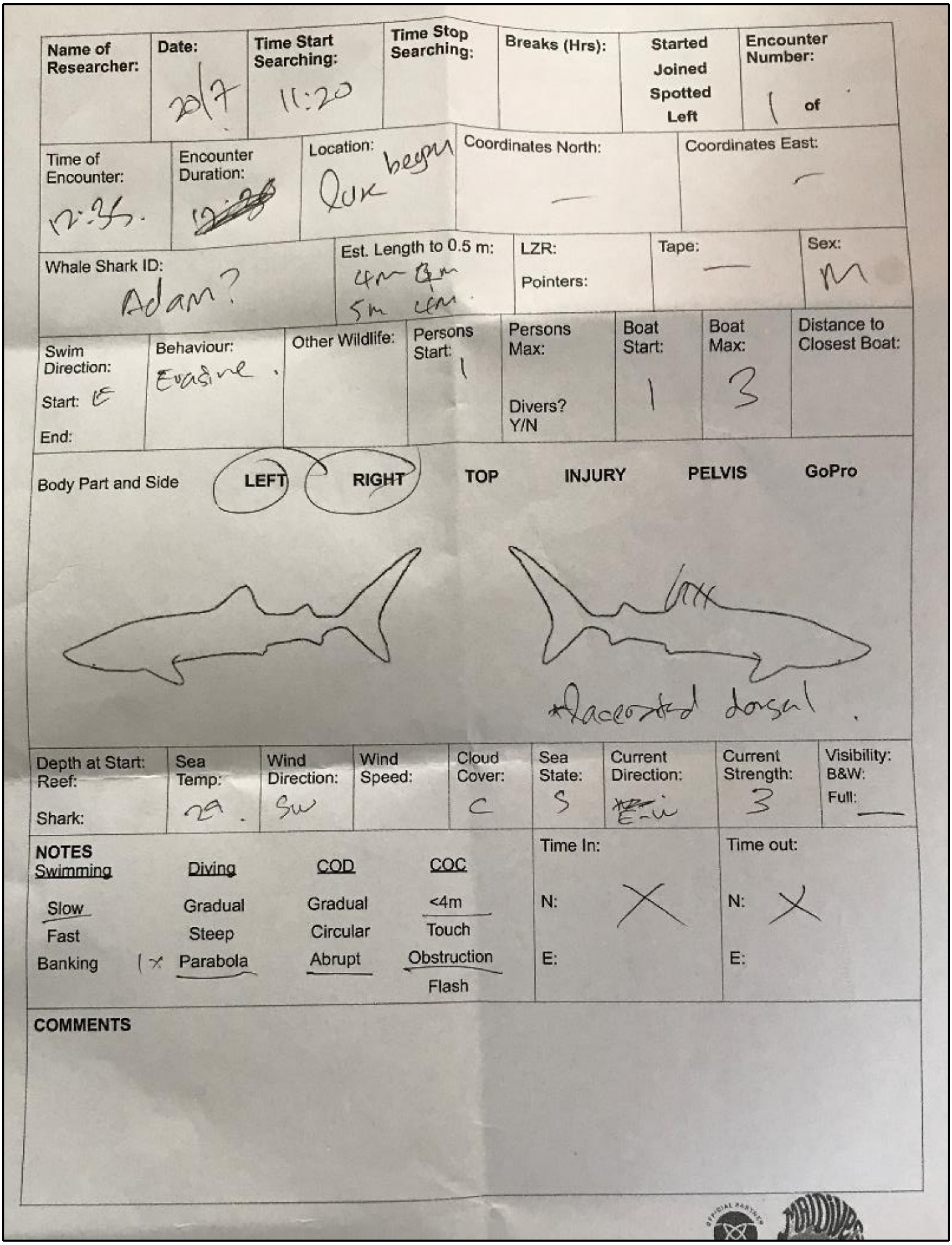


Figure 17: Chlorophyll a concentrations at SAMPA. Chlorophyll a was calculated by utilising the SAMPA template to extract all chlorophyll a values within the study site from which a mean was calculated for each eight-day composite.



Name of Researcher:	**Date:** 20/7	**Time Start Searching:** 11:20	**Time Stop Searching:**	**Breaks (Hrs):**	**Started** **Joined** **Spotted** **Left**	**Encounter Number:** 1 **of**

Time of Encounter: 12:35.	Encounter Duration: ~~[illegible]~~	Location: Qux began	Coordinates North: —	Coordinates East: —

Whale Shark ID: Adam?	Est. Length to 0.5 m: 4m 6m 5m len.	LZR: Pointers:	Tape: —	Sex: M

Swim Direction: Start: E End:	Behaviour: Evasive.	Other Wildlife:	Persons Start: 1	Persons Max: Divers? Y/N	Boat Start: 1	Boat Max: 3	Distance to Closest Boat:

Body Part and Side [✓ **LEFT**] [✓ **RIGHT**] **TOP** **INJURY** **PELVIS** **GoPro**

laxx

*lacerated dorsal.

Depth at Start: Reef: Shark:	Sea Temp: 29.	Wind Direction: SW	Wind Speed:	Cloud Cover: C	Sea State: S	Current Direction: ~~[illegible]~~ E-W	Current Strength: 3	Visibility: B&W: Full: —

NOTES __Swimming__	__Diving__	__COD__	__COC__	Time In:	Time out:
[✓ Slow]	Gradual	Gradual	[✓ <4m]	N: X	N: X
Fast	Steep	Circular	Touch		
Banking	(x [✓ Parabola]	[✓ Abrupt]	[✓ Obstruction]	E:	E:
			Flash		

COMMENTS

Figure 18: Whale shark encounter form displaying the environmental variables collected during each encounter

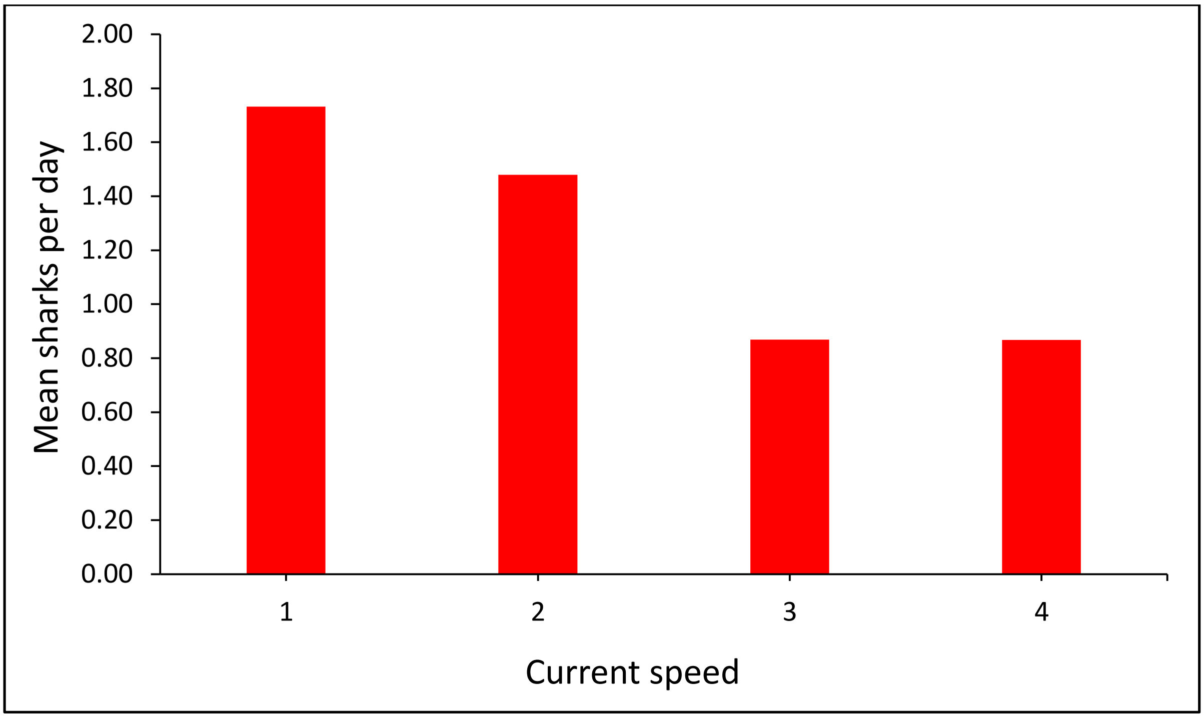


Figure 19: Current speed showing a significant negative relationship with mean sharks per day (Current speed 1 = 1.73, 2 = 1.48, 3= 0.87, 4 = 0.88).