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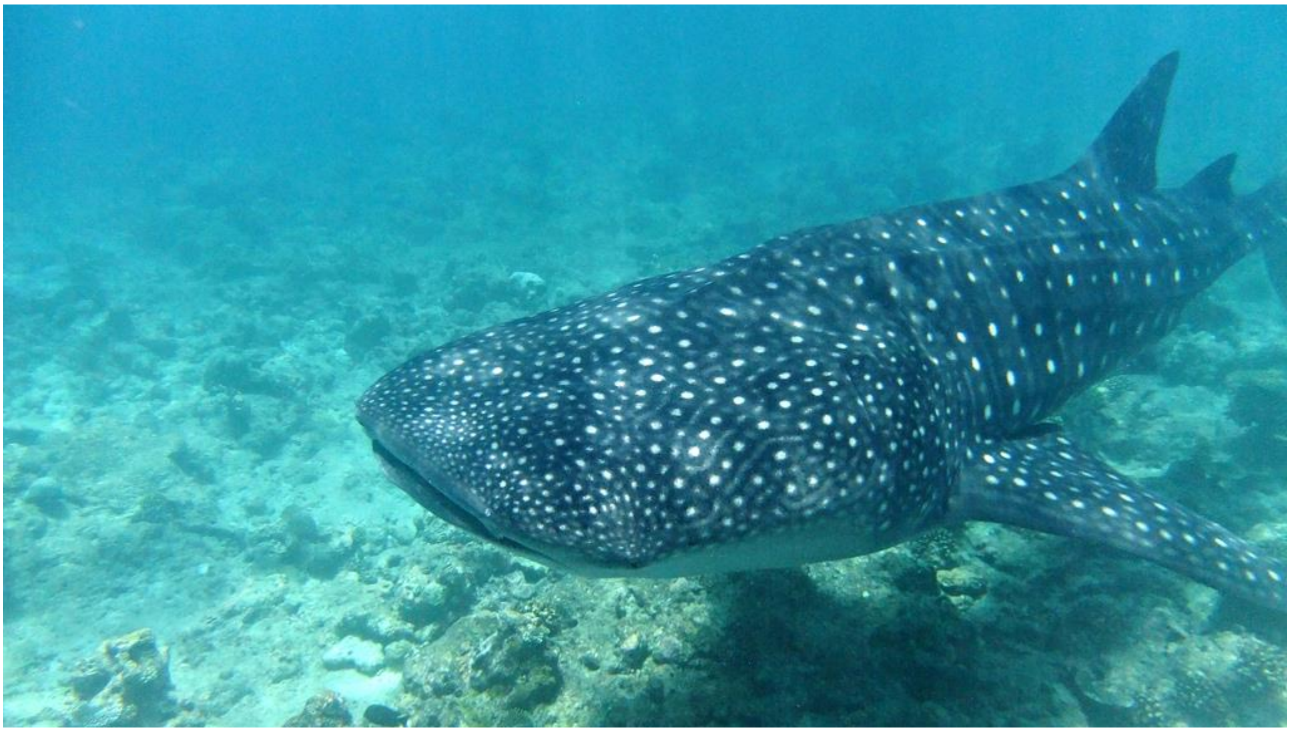
Whale shark movements between atolls in the Maldives



Isabelle Eady

MSc Dissertation in Marine Environmental Management

Disclaimer

I hereby state that the work within this dissertation was solely my own and all analysis was undertaken by myself. All sources used in this work have been sufficiently sighted.

Acknowledgements

First and foremost I would like to thank the Maldives Whale Shark Research Programme (MWSRP) for generously providing me with the primary data for this study and the concepts behind it. Also to Jim and Richard of MWSRP for their knowledge and answering my various emails on the topic. I would also like to thank Dr Bryce Beukers-Stewart for his supervision and guidance on my dissertation, and would like to acknowledge support from my other advisor Dr Colin McClean.

Abstract

The Maldives is home to a large number of whale sharks, *Rhincodon Typus*. Much is known of the year round aggregation site in South Ari atoll, whose residents are protected by Marine Protected Area. Development of the citizen science network has enabled understandings of the distribution of the Maldives on a whole to be documented, and found that sharks are seen not only in Ari but across the island chains. However, movements in these areas are poorly understood. The aims of this therefore study were to identify sharks in other atolls, assess movement, and link this movement to environmental variables. The whale shark encounter data used in this database were collected by the Maldives Whale Shark Research Programme and citizen scientists spanning from 1992 to 2018. 13 environmental variables were modelled with sightings of moving sharks through subsets using Generalized Additive Models. 8 predictor variables were found to be significant, with 39.3% of variance explained by Oceanograhic variables *atoll* and *distance to seamount* while Temporal variables *Time, month and year* explained 21.1%. Indian Ocean Dipole Index, Sea Surface Temperature and chlorophyll-a combined accounted for only 2.85% of the variance. Whale sharks exhibited defined bi-annual movement between monsoons, and seasonal presence at all atolls other than South Ari. Seasonally alternating currents likely bring food resources distributed to different atolls that either become more or less suitable for whale sharks. Further research through satellite tagging is needed to confirm movements, and biomass samples carried out to quantify changes in prey species.

1. Introduction
1.1 Background

The whale shark, *Rhincondon Typus,* is one of only three living filter feeding species of shark, reaches up to 18m in length (Compagno, 2001), and was only scientifically identified in 1828 from a sighting off the Cape of Good Hope, South Africa (Bean, 1901). Once worshipped by the Polynesians and "*considered to be allied to Leviathans of the deep*" in the 1600s, documentation of the whale shark has changed the once fearful opinion for it to a fascination (Bennett, 1834). Although displaying a likeness to its plankton feeding counterparts, this species belongs to the orectolobiformes, making its closest relatives other carpet sharks such as the nurse shark. Carpet sharks display behavioural learning, making them a highly intellectual organism deserved of further study (Dudgeon & White, 2012, Thomson et al., 2017).

Whale sharks reach sexual maturity late in life, and their slow growing (and moving) characteristics make them vulnerable to exploitation. Their rarity was first officially recognised when they were listed on the IUCN Red List as vulnerable in 2003. However, some populations have reduced in size by >50% (Pierce & Norman, 2016). Not only is their abundance falling, but their average size is, too, with sharks at Nigaloo Reef today nearly 2.0m smaller than those found a decade ago (Bradshaw, 2008). For this reason, whale sharks were recently re-listed as endangered (Pierce & Norman, 2016)

1.2 Distribution & aggregations

As a large marine animal feeding on very small prey, whale sharks need to consume considerable quantities of food to sustain energy demands. Foraging behaviour is important to this species, but *R.typus* lives within the nutrient poor waters of the tropics, where plankton abundance is highly variable in space and time. Nonetheless, whale sharks have been recorded gorging on zooplankton communities (Marliana et al., 2018), small shrimps (Rohner et al., 2015), copepods, fish spawn (Heyman et al., 2001) and juvenile crabs (Hobbs et al., 2009).

The whale shark is found regularly in between 30°N and 35°S with infrequent seasonal sightings elsewhere (Turnbull and Randell, 2006). Very few predictable feeding aggregations occur. An aggregation is that of more than 10 sharks in less than 1km^2 of ocean (Rowat & Brooks, 2012). So far 20-25 sites have been identified (Pierce & Norman 2016, Copping et al., 2018). Most aggregations are seasonal and consist of immature, juvenile males, with only Galapagos consisting of female sharks (Acuña-

Marrero et al., 2014). 2001).

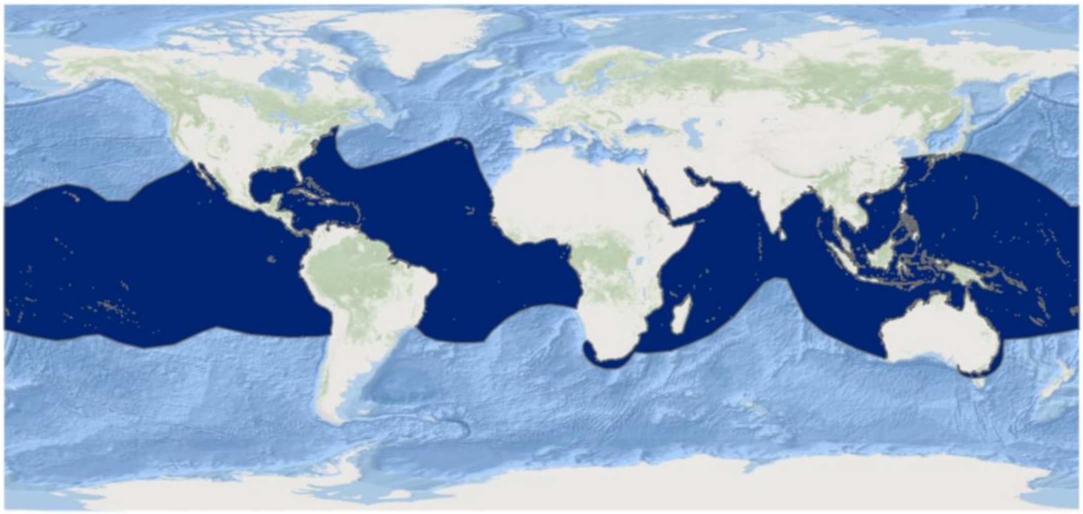


Figure 1: Distribution of Rhincodon. Dark blue shape represents distribution (data provided by IUCN RedList, 2018).

1.3 Environmental & biological variables

Sea Surface Temperature (SST) and chlorophyll-a play an important role determining where whale sharks are found. Higher sea surface temperatures have been linked to whale shark distributions (Robinson et al., 2017), with habitat suitability for whale sharks in the Indian Ocean correlation with variations in temperature (Sequira et al., 2012., Sequira et al., 2014). Sharks only found at the limits of their geographical range when oceanographic conditions result in warmer than normal waters (Afonso et al., 2014). Chlorophyll a is linked to zooplankton abundance and thus weak links between whale sharks occur (Sleeman et al., 2010)

Aggregation sites are shallower, steeper and closer to deep water than non-aggregation sites (Copping et al., 2018), while studies have found associations between whale sharks and proximity to seamounts (Afonso et al., 2014). Whale sharks are known to exhibit deep diving behaviour linked to these bathymetric features in search of prey (Brunnschweiler et al., 2009), with diel migration into bathypelagic zones hypothesised to represent foraging events in the deep sea (Tyminski et al., 2015).

Association with upwelling fronts, currents and eddies is also characteristic of whale sharks (Ryan et al., 2017., Sleeman et al., 2010., Taylor et al.,1999). Links with oceanographic index's and whale shark distribution also occur. In La Niña years ENSO years, greater numbers of whale sharks occur at Nigaloo Reef, Australia (Wilson et al., 2001), and are closely associated with the Southern Ocean Index (Sleeman et al., 2010). Positive NAOs in the Azores result in an increased in probability of whale shark appearance (Afonso et al., 2014)

1.4 Movement

Movements of whale sharks display spatio-temporal plasticity (Eckert et al., 2002), moving in response to environmental/habitat changes, predator avoidance and mating opportunities. Relatively little is known about geographical ranges of *individual* whale sharks, but some have been recorded moving very large distances. Hueter (2013) recorded a female whale shark moving approximately $7772km^2$ in under 5 months, while Diamant recorded a whale shark moving 4275 km^2 across Madagascar (2018). Other studies have found connectivity between aggregation in the Indian Ocean; from Mozambique to South Africa and Mozambique and the Seychelles (Gifford et al., 2007, Brunnschweiler et al., 2009).

Studies of animal movement were revolutionised in the 1970s through the arrival of satellite tagging technology, giving insight into whale shark diving behaviour, horizontal movements and “migrations” (Brunnschweiler et al., 2009). However, tagging can be costly and comes with technological disadvantages such as tags loss and malfunctioning.

Citizen science (CS), where the general public is called on to gather data, presents a significantly cheaper alternative to tracking through space and time. With advancements in handheld devices with in-built GPS systems (e.g. mobile phones, cameras) citizens can now contribute to research. For whale sharks, CS has been able to track demographics, movement and connectivity of species (Heuter et al., 2013, Mckinney, 2013). The whale sharks appearance makes them an attractive animal for ecotourism and easy for the everyday citizen to spot, photograph and document. Furthermore, their unique spot pattern remains unchanged for decades, providing a reliable way to ID sharks.

1.5 Motivations for research

The Republic of the Maldives is a small island nation in the Indian Ocean. An important aggregation of whale sharks is found here; specifically in South Ari, which persists all year round (Donati et al., 2016, Cagua et al., 2014). Like most aggregations, Aris sharks are mostly male juveniles (Riley et al., 2010), having the highest ratio of Males to Females than other aggregations in the Indian Ocean (Andrzejaczek et al., 2016). A localised research programme, the Maldives Whale Shark Research Programme (MWSRP), dedicated to studying this aggregation has existed in Ari since 2006, using photo-identification techniques to discover what might be driving this aggregation. A marine protected area (MPA) exists specifically to protect this aggregation that is worth £9 million to the local economy each year (Cagua et al., 2014).

The MWSRP utilises CS through the Big Fish Network. This is a CS ‘app’ where researchers, resorts and the public upload pictures of their interactions with whale sharks in the Maldives. Through this and Wildbook for Whalesharks, sharks have been reported at atolls other than Ari, with some displaying inter-atoll movement. Research conducted by Ahmad and Anderson in 1993, who distributed questionnaires to fishermen whom provided an estimate of whale shark distribution in the Maldives (Figure 2). They hypothesised that sharks were located in northern atolls in the Southwest monsoon, and moved to southern atolls in the Northeast to take advantage of seasonal prey movements. This begs the question as to whether the MPA at Ari affords sharks protection at all.

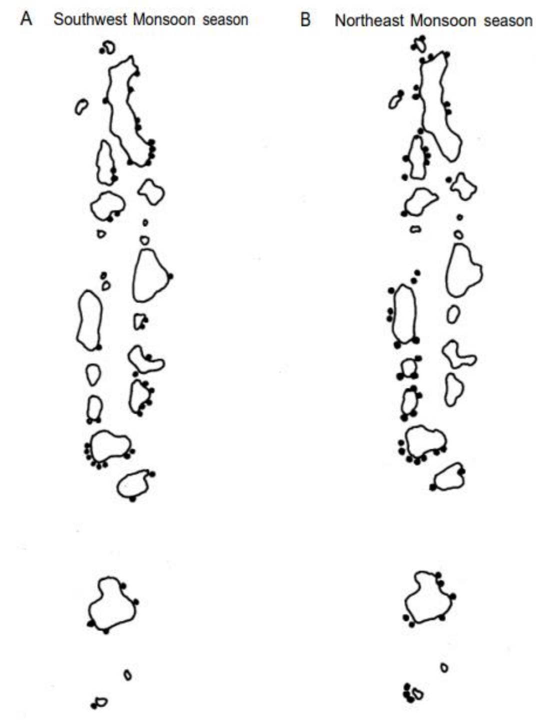


Figure 2: Whale shark distribution as derived by questionnaires of fishermen (Anderson and Ahmad, 1993)

Evidence of continued hunting of this species in the Maldives has arisen in recent years, and combined with a declining population, understanding these movements is of great importance (Riley et al., 2009).

1.6 Aims

This project aims to utilise citizen science data on whale sharks in the Maldives to determine movements of sharks between atolls and discuss the environmental variables driving these movements. This was achieved by setting the following objectives:

- Determine the most common movement
- Investigating seasonal changes to movement
- Identifying variables significant to sightings of moving whale sharks.

2. Methodology
2.1 Setting of research

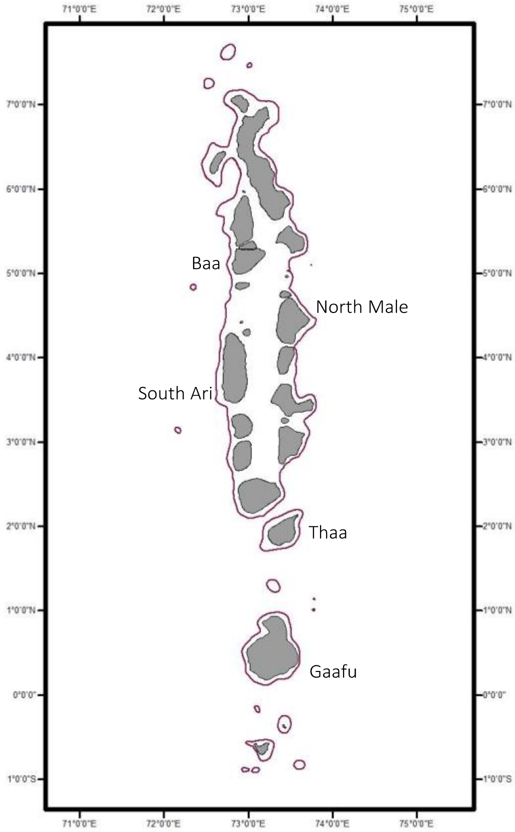


Figure 3: Map of the Maldives with atolls mentioned in text. The outer lines represents the 1000m depth contour line. 1 degree latitude = 111km

The Maldives (Figure 3) is a 900km area of the Indian Ocean composed of many coral atolls, which form a paired chain running north-south from 07º6’30”N, 72º32’30”E to 00º41’48”S, 73º45’54”E (Sasamal, 2007). This isolated carbonate platform lies southwest of Southern India, on a 100km wide submarine ridge with an enclosed basin named the 'Inner Sea'. This area is characterised by rapidly descending external slopes that reach the abyssal and bathyal depths of the Indian ocean rapidly (Lüdman et al., 2013). The nation has 21 atolls, and over 1200 coral reef islands that originate from the Holocene period (Sundulli et al, 2014). Discontinuous marginal rims surround island lagoons with water depths of up to 60m, which are then interrupted by deep passages that allow for strong current regimes with lagoons (Betzler et al., 2012).

The Maldives experience 2 monsoonal seasons; in boreal winter (December – April), the northeast monsoon flows from east to west, southward of Sri Lanka (Anderson et al., 2011), creating the North Equatorial Current. During May to November, strong winds from the Southwest, combined with increased precipitation and storms define the southwest monsoon. Currents are directed eastward during this monsoon season. While monsoons majorly influence current regimes, circulation is varies between years, having been linked to ENSO events (Longhurst, 2007).

Northern atolls are dominated by strong inflows of Indian Ocean Water through the NE Kardiva channel, flowing southwest and reach velocities of 40cm/s. Two major currents meet between South Ari and North Male and form a prominent collision front that creates anti-clockwise eddies (Lüdman et al., 2013). The Indian Ocean Water that enters the Inner sea at depth has low oxygen, but high nutrient concentrations.

2.2 Whale shark sightings data

Data were provided by MWSRP, which included a compilation of data from Wildbook for Whale sharks, the Big Fish Network and data from MWRSP research programme. Data extended from 1992 to February 2018, and included information on the location (GPS coordinates), date and time of a sightings, as well as estimated size, sex, behaviour, current strength. For simpler analysis, the latter data were excluded during analysis as on multiple occasions these was not recorded.

Sharks from 5 other atolls were identified and used in this study and highlighted in Figure 3; these were Baa, North Male, South Ari, Thaa and Gaafu.

2.3 Data Analysis

To test the hypothesis based on Ahmad and Anderson (1993) that whale sharks are primarily seen to move seasonally between monsoons to different atolls, it was necessary to analyse all sightings data and determine whether there was a relationship between the season and location of whale sharks records. The null hypothesis would be that whale sharks are evenly distributed between atolls, irrespective of season. In practice, sites where whale sharks are not expected to be seen are less frequently visited, however despite there being year round observers in atolls, whale sharks only appeared at certain times (pers.comms).

To assess movement patterns, sharks seen only once and in one atoll were excluded from movement analysis and subsequent statistical analysis. To assess movement in relation to environmental influences, the remaining sightings were grouped into monthly sighting records (monthly sightings per atoll) for ease of modelling.

2.4 Statistical analysis

Statistical analysis were carried out using R (version 3.5.0; http://cran.r-project.org). Predictor variables included for statistical analysis are given in Table 1.

To account for temporal influences on whale shark sightings, time of day, month and year were included for analysis. Atoll was included as a predictor in whale shark models because whale sharks were observed at 5 different atolls, and was used to investigate any preferences for certain atolls (as in Rohner et al., 2013). Remotely sensed chlorophyll a concentration (chla) was downloaded from NASA's Aqua Modis Satellite as a proxy for food availability in an area lacking sufficient zooplankton data. Despite the knowledge of a time lag that is seen between phytoplankton abundance and zooplankton blooms chl-a concentration has in the past been linked to whale shark and movements. Particulate Inorganic Carbon content (PIC), Particulate Organic Carbon Content (POC) and Sea Surface Temperature (SST) was also derived from Aqua Modis (NASA, 2018). The Indian Ocean Monsoon Index (herein known as DMI) data were downloaded from JAMSTEC. Sea Level anomalies were downloaded from AVISO (http://www.aviso.altimetry.fr/), however prior to modelling it was found that this cut off 04/2017 and it was not included. Bathymetry and slope (°) were derived from the General Bathymetric Chart of the Oceans (GEBCO, 2018) at a 1km, 30 arc-second interval global grid. Seamount location data was downloaded from Kitchingman and

Lai (2004); distance of sightings to seamounts was derived using the *Near* tool in ArcGIS.

These were modelled against sightings per month (per year) per atoll. Prior to statistical modelling, chlorophyll a and POC were transformed to account for strong skew (log(log) and log+1). Testing for heteroscesadicity found no significant variance. Intercorrelation between chlorophyll a and POC led to removal of POC. No significant correlation through VIF and Pearson was found in other variables, and a negative binomial generalised linear model was deployed on the data. The 'Use Your Brain' method was deployed to create three Models; temporal, environmental and oceanographic sets. This method was chosen to increase statistical rigour (Burnham and Anderson, 2010).

Table 1: Predictors used in the generalized additive models (GAMs) for whale shark movements

Variable	Parameter	Explanation	Type	Units
Response	**Whale Shark sightings**	Sightings per month		
Predictors	SST[a]	Sea Surface Temperature	Continuous	°C
	Chl-a[a]	Chlorophyll-a concentration (monthly mean)	Continuous	mgm^{-3}
	POC[a]	Particulate Organic Carbon (monthly mean)	Continuous	mgm^{-3}
	DMI[b]	Indian Ocean Dipole (index)	Categorical	-
	PIC[a]	Particulate Inorganic Carbon (monthly mean)	Continuous	mgm^{-3}
	Depth[c]	Depth observation (derived from bathymetry)	Continuous	m
	Distance to seamount[c]	Derived from bathymetry	Continuous	km
	Slope[c]	Derived from bathymetry	Continuous	Degrees
	SSH[d]	Sea Surface Height (monthly mean)	Continuous	m
	Time	Time of observation (average)	Continuous	hh
	Month	Month of observation	Categorical	mo
	Year	Year of observation	Categorical	yr
	Atoll	Location of observation	Categorical	Levels: 1 (Baa), 2 (Gaafu), 3 (North Male), 4 (South Ari), 5 (Thaa)

[a]Aqua Modis Satellite, b JAMSTEC [c]GEBCO, [d]AVISO

Generalised Additive Models (GAMs) with a poisson error function were used to investigate the predictor variables influence on whale shark sightings. Both multivariate and univariate GAMs were checked for overdispersion. Model goodness of fit was evaluated based on the deviance explained by each model. GAMs were reduced to Minimum Adequate Models using Akaike's Information Criterion. Analysis of deviance (anova) using a Chi squared test were applied to each MAM to check that reduced models did not lose significant variance over the full models.

3.5 GIS analysis

All GIS analysis was computed through ArcMap 10.5.1. Sightings were overlaid with relevant environmental variable shapefiles in both spatial and temporal resolution. A 2km buffer was created around each sighting and then *sampled* to deduce the values for the environmental variables these fell into. Bathymetric data from the area was overlaid and maximum depth of sighting point deduced. Slope (degrees) was calculated through spatial analyst tools, and distance to closest seamount of each sighting recorded.

Chl-a maps for the Northeast monsoon and Southwest monsoon were created through binning the months of each monsoon (Dec – March for northeast, June – November for southwest) using the *mosaic to new raster* function to create 2 maps to compare from.

Sequences of individual whale shark sightings were investigated to determine patterns of movement and estimated distances covered during seasonal movement. Case studies of examples of these movements of individual whale sharks are described in Appendix but not included in the main body of text. While it cannot be determined that sharks followed these distinct paths, it gives an understanding of the patterns of movement in sightings.

3. Results

3.1 Distribution

In total, 4468 photographs were collected for this study spanning from 1992 to 2018, from MWSRP, the Big Fish Network and Wildbook for Whalesharks. From these, 355 individual sharks were identified at 5 different atolls from North to South; Baa, South Ari, Male, Thaa and Gaafu as highlighted in Figure 3. Of the 355 individuals, 192 were re-sighted at least once (54.08%), with the remaining 163 (45.92%) seen once only. Sightings data for each atoll is summarised in Table 2.

74.93% of individual sharks from the database were found in South Ari. Gaafu had the second largest number of sharks entering its waters (n=47), and Male the fewest (n=18). All atolls had whale sharks that were only seen in that particular atoll.

Sharks were seen year round in Ari, with no significant peak in shark sightings in any one month. However, there was a strong indication that sharks were largely seasonal in other atolls (Figure 4). In Baa, most whale sharks were sighted between July and October during the Southwest monsoon period. Thaa and Gaafu, the reverse occurred with most sightings recorded in the northeast monsoon from May to November (Figure x). In Male, sightings were the lowest of all atolls, although peaked in the inter-changing monsoon period (Nov).

1623 sightings (36.3% of all records) were recorded of sharks moving between atolls between March 2006 to February 2018. This equates to 14% of the individual sharks (n=47) ever recorded in the Maldives, and 24.58% of sharks that were recorded more than once (n=192). Of the sharks moving, only >2% were seen in more than 2 atolls.

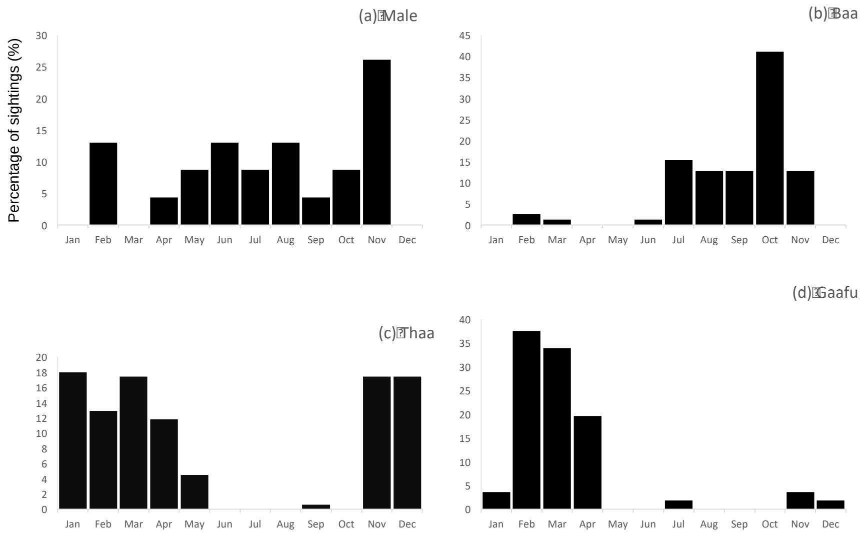


Figure 4: Percentage of sightings in each month at atolls where sharks were seasonal

Table 2: Number of individual whale sharks known at each site, percentage of total population (n=355), individuals re-sighted (and percentage re-sighted) and individuals seen in multiple atolls

Atoll	**Whale shark IDs**	**% of total population**	**Ever re-sighted**	**% re-sighted**	**Multiple atolls**
Baa	45	12.68	28	62.22	23
North Male	18	5.08	11	61.11	10
South Ari	266	74.93	165	62.03	42
Thaa	33	9.30	29	87.88	18
Gaafu	47	13.40	14	29.79	6

3.2 Movement

3.2.1 Monsoonal movement

Figure 5 shows movement between monsoons. In the Southwest monsoon, sharks are most regularly seen in Southern atolls, on the Eastern side of Western atolls. Distribution shifts in the Northeast monsoon, with more sightings on Easter atolls and the Western site of western atolls. Sightings of sharks move south; a greater proportion of sightings occur in the Southern most atolls (like Gaafu).

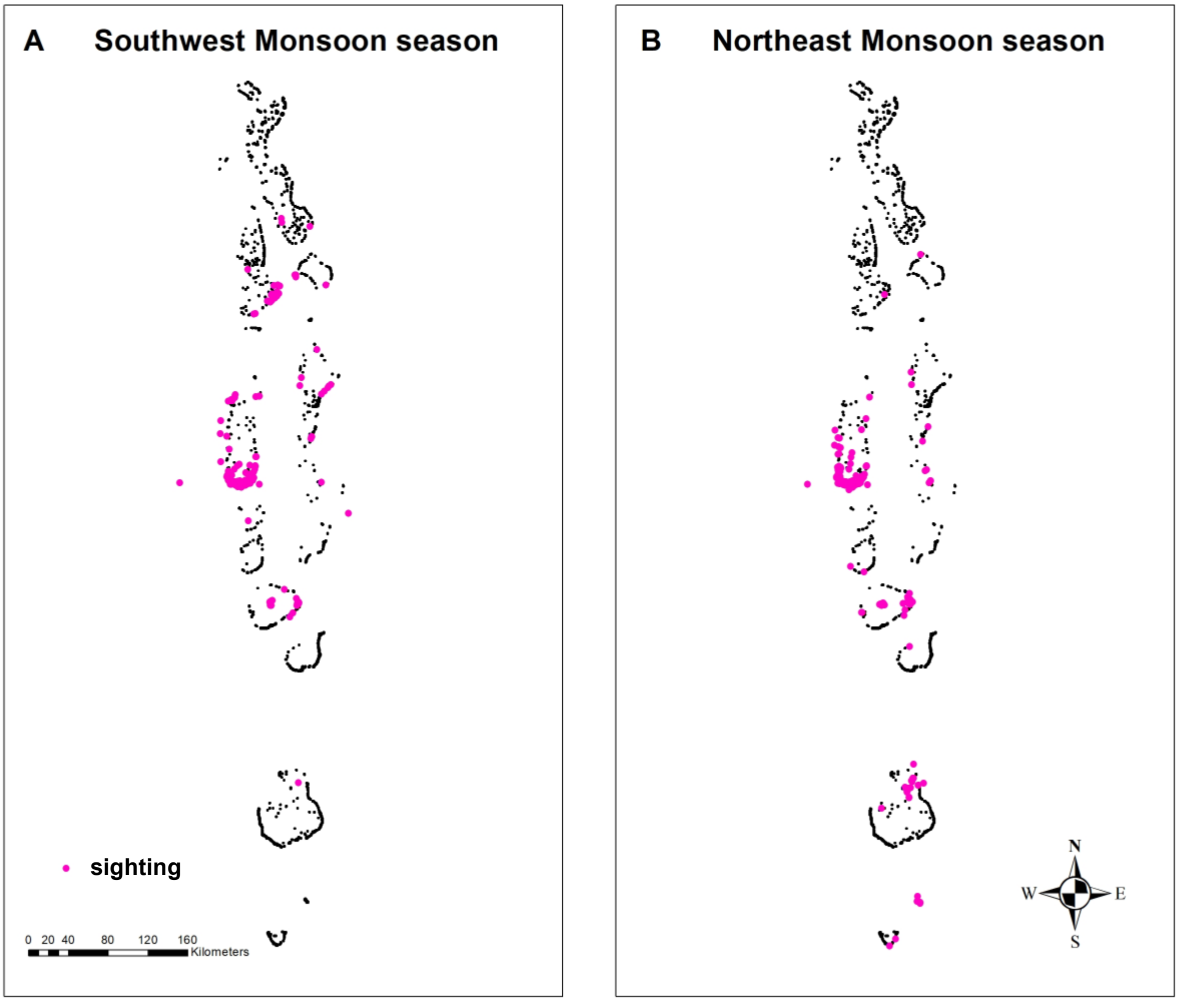


Figure 5: Seasonal change in sightings for whale sharks in the Maldives. Sharks are found in Northern atolls on Western sides in the Southwest monsoon, and are sighted in Southern atolls on the Eastern sides in the Northeast monsoon.

3.2.2 Atoll movement

The number of whale sharks recorded showing atoll movement is listed in Table 3. Sharks exhibited 6 main types of movement (Figure 6) between atolls. 17 sharks showed inter-atoll movement between South Ari and Baa. This represents 36% of the moving sharks, and the most common movement between atolls. 15 sharks exhibited movement between South Ari and Thaa (32%). 19% showed movement between Male and Ari. Almost all of the moving sharks showed up in Ari at some point; only 8.5% of the sightings of moving sharks were of sharks that never entered Ari (n=4).

Table 3: Number of whale sharks seen at different atoll combinations and whether these movements followed the northeast or southwest monsoon

	Atoll Movement					
	South Ari - Baa	**South Ari - Thaa**	**South Ari - Male**	**South Ari - Gaafu**	**Baa - Thaa**	**Baa - Male**
Individual (Whale Shark Identification)	WS000 WS005* WS010* WS012* WS017* WS025* WS039* WS057* WS059* WS089* WS178* WS187* WS195* WS206* WS209* WS222* WS340*	WS000 WS014 WS030* WS106* WS189* WS196* WS200* WS209* WS212* WS214* WS229* WS286* WS294* WS295* WS302*	WS000 WS067* WS077* WS111* WS157* WS174* WS177* WS183* WS266*	WS000 WS171* WS186* WS199* WS236*	WS000 WS014 WS209 WS255* WS268* WS275*	WS000 WS321*
Total individuals	**17**	**15**	**9**	**5**	**6**	**2**
Percentage (%)	**36.17**	**31.91**	**19.15**	**10.64**	**12.77**	**4.26**
Seasonal?	**Southwest**	**Northeast**	**?**	**Northeast**	**Northeast**	**?**

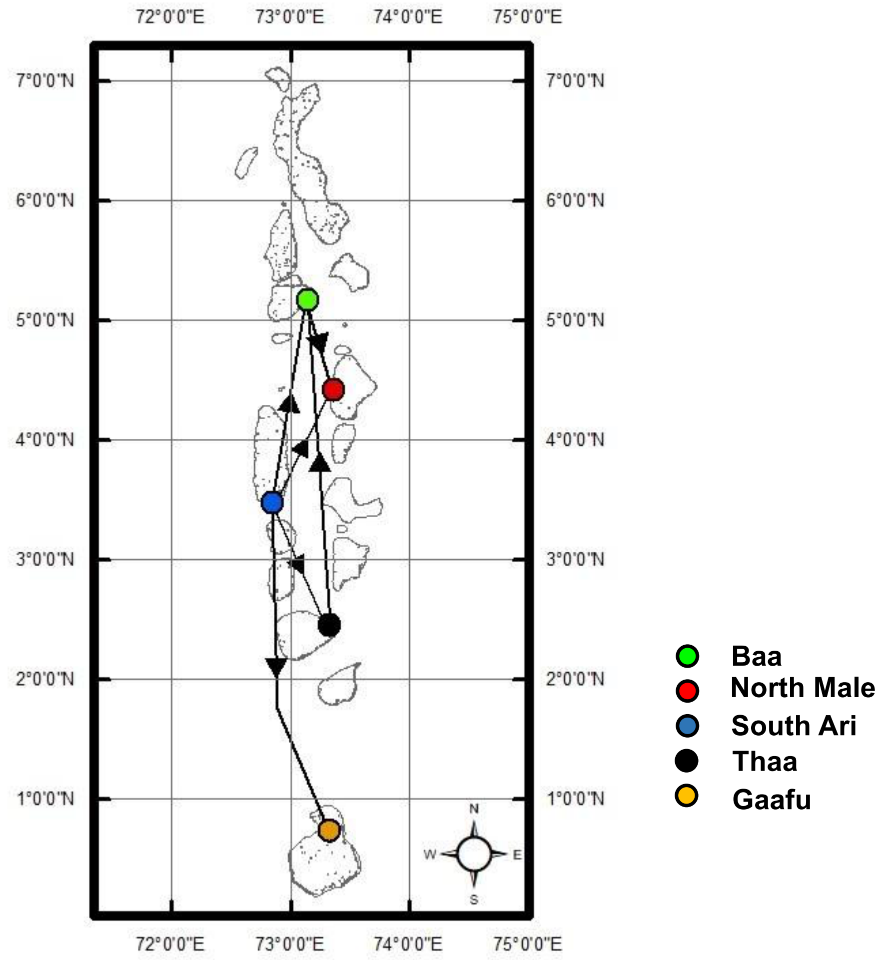


Figure 6: Most common movements recorded through sightings.

3.3 Environmental variables

Summation of the statistical analysis and GAMs performed with response variable 'sightings per month' are given in Table 4 and used to explain movement. Multivariate models, instead of univariate ones were selected in all 3 of the modelled subsets. Models with low AIC, high %D and wi were the most significant in driving variation within of whale shark sightings. Of the temporal set, all variables were retained and accounted for 21.1% of the variance in sightings. Higher SST and chl-a concentrations were correlated with higher sightings, while DWI negatively influenced variance. These three variables accounted for a low 2.85% of the total variance. 2 minimum adequate models were found to have the same significance for the Oceanography set (with AIC within 2 of eachother); Atoll and Seamount accounted for 39.1% of the variance, while Atoll, Seamount and Slope together explained 39.3%; Slope was not considered a significant variable ($p > 0.001$) however was included to emphasise its influence on %D. In total, 63.25% of the variance was explained by the predictor variables. Influence of each retained variable on whale shark sightings is given graphically in Figure 7.

Table 4: Generalized Additive Model results for each subset of predictor variables on sightings per month

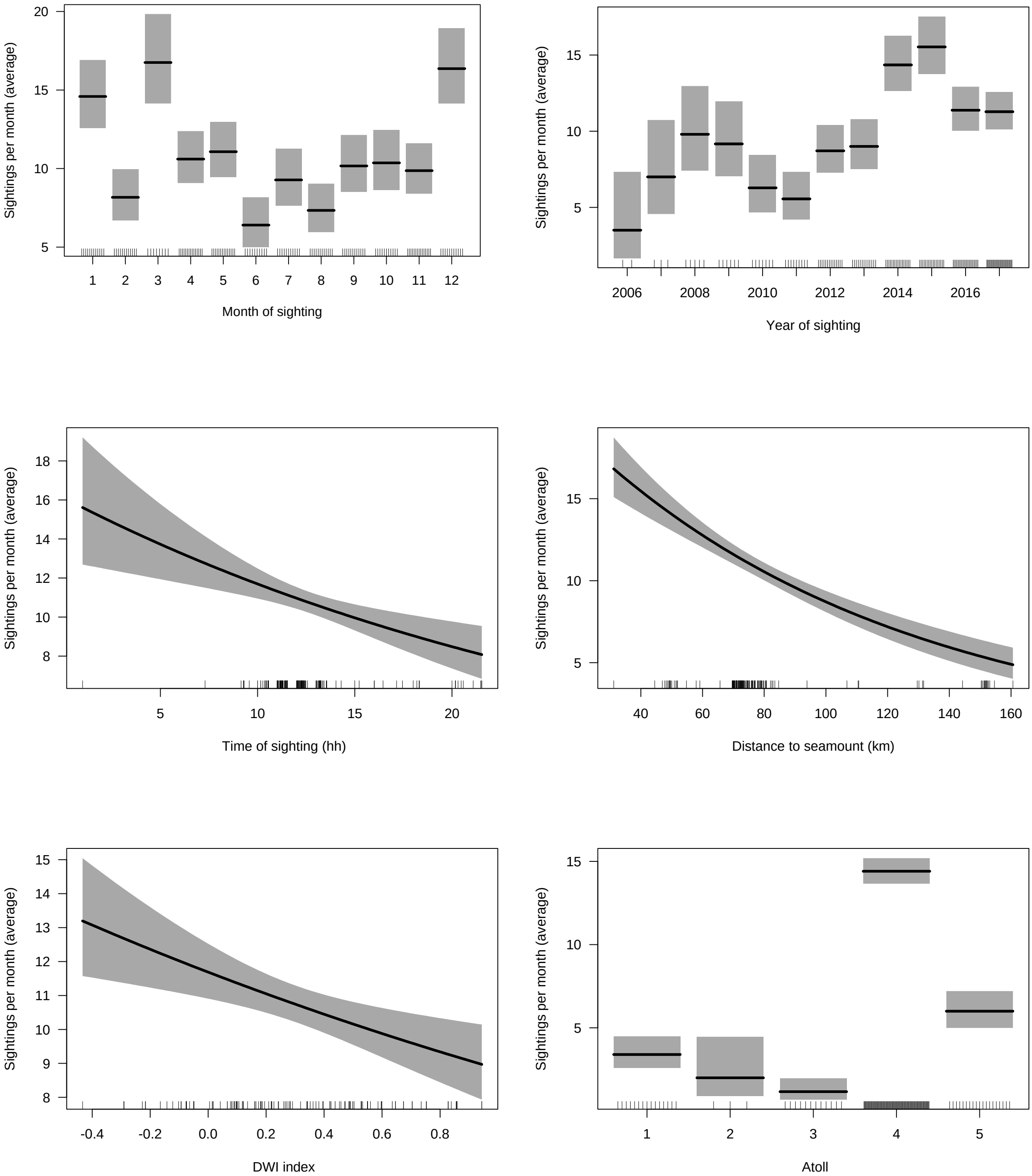
Significant Variables	Test statistics	P value
Multivariate GAM (the minimum adequate models)		
[a] Month, Year, Time (-)	AIC=1526.7, %D=21.1, Wi=1	<0.001, <0.001, <0.001
[b] SST (+), ln ln Chl-a (+), DWI(-)	AIC=1705.7, %D=2.85 Wi=0.7004	<0.001, <0.001, *0.003*
[c] Atoll (+), Seamount (-)	AIC=1275.5, %D=39.1 Wi=0.4017	<0.001, <0.001
[c] Atoll (+), Seamount (-), Slope (-)	AIC=1275.9, %D=39.3 Wi=0.3187	<0.001, <0001, *0.212*

- [a]Temporal set: Month, Year, Time
- [b]Environmental set: SST, ln ln chl-a, PIC, DWI
- [c]Oceanography set: Bathymetry, Slope, Atoll, Distance to Seamount

Ln=natural log
The direction of the trend (+/-), percentage deviance explained (%D), Akaike Information Criterion (AIC) and Akaike weight (Wi) are included.
Minimum adequate models did not show reduced deviance from full models (Analysis of Deviance: p = 0.434-0.606)

Sightings show a seasonal trend with more sightings generally in northeast monsoon months. Fewest sightings of all atolls were in Southwest monsoon periods (June, August) and highest in January, April and December. Time of sighting influenced how many were seen, with most sightings from 10:00 to 13:00 hh. Distance to seamount impacted whether a shark was sighted; fewer sightings were recorded furthest from seamounts. The Indian Ocean Monsoon Index was a slightly significant variable (0.003), with a higher index resulting in fewer sightings. Atoll was a significant predictor in whale shark sightings, with its model accounting the highest deviance explained (39.1%). Most sightings (and the highest per month) were seen at atoll 4 (South Ari), followed by Thaa, and lowest at North Male.

SST and chl-a were strongly significant predictors for sightings. Warmer, chlorophyll rich waters had a positive effect on sightings. However, these variables accounted for only 2.85% of the deviance. Composite satellite chl-a concentration for the Maldives in each monsoon and subsequent sightings is given in Figure 8. Higher chl-a values are found on the downstream of the currents direction for atolls in each monsoon, and show a reversal of sides with the different monsoons.


Sightings per month (average)
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12
Month of sighting
Sightings per month (average)
15
10
5
2006 2008 2010 2012 2014 2016
Year of sighting
Sightings per month (average)
18
16
14
12
10
8
5 10 15 20
Time of sighting (hh)
Sightings per month (average)
15
10
5
40 60 80 100 120 140 160
Distance to seamount (km)
Sightings per month (average)
15
14
13
12
11
10
9
8
-0.4 -0.2 0.0 0.2 0.4 0.6 0.8
DWI index
Sightings per month (average)
15
10
5
1 2 3 4 5
Atoll

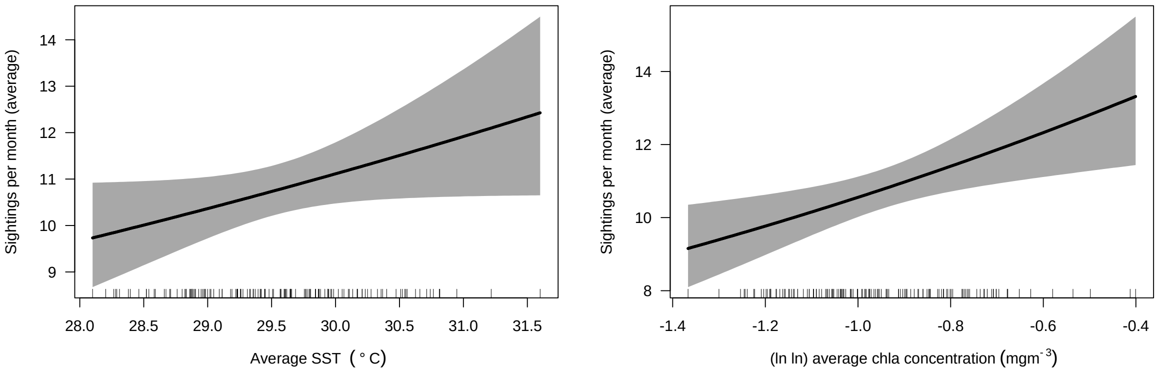
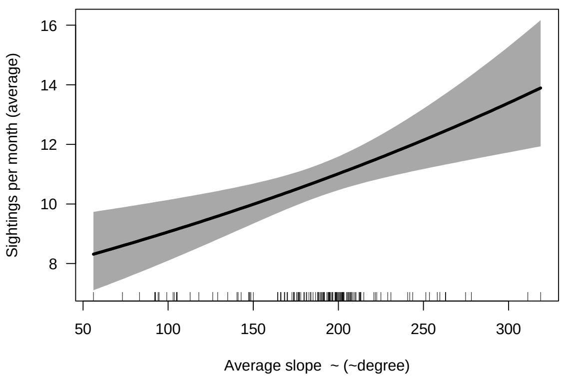


Figure 7: Whale shark (Rhincodon typus) GLM model outputs showing relationship between monthly sightings and all significant predictors. The rug plot along the x-axis indicates the sampling effort and shaded bands prepresent the 95% confidence intervals. See Table 1 for details



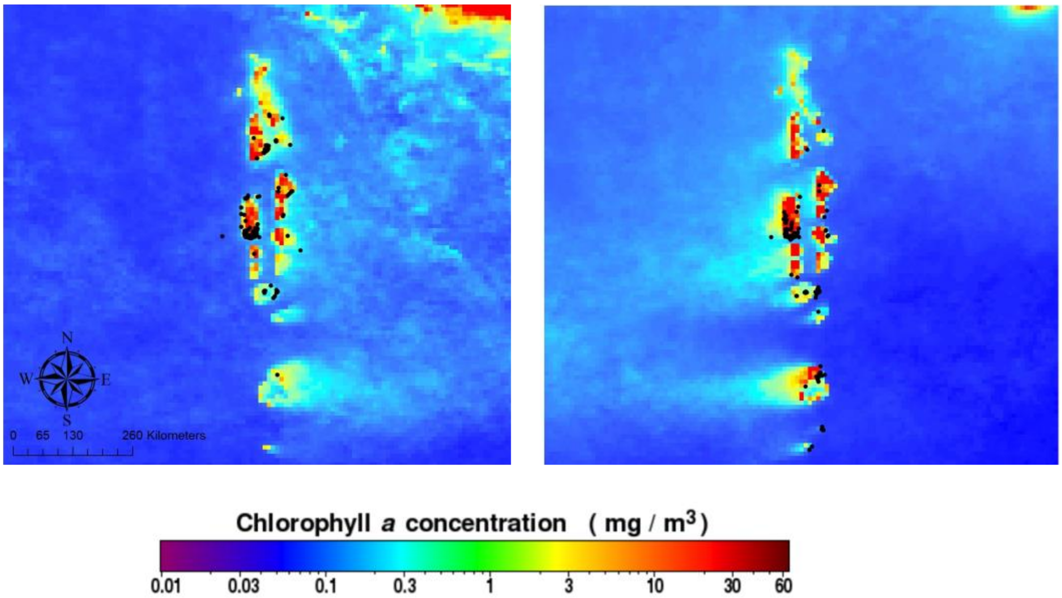


Figure 8: Binned chlorophyll a content from Aqua MODIS satellite data. Two monsoons displayed; on the left the soythwestt and on the right the northeastt. black dots represent shark sightings

4. Discussion

4.1 Environmental

Predictors explained >62% of the variance in sightings, with the oceanographic set explaining the most. A recent paper found that aggregation sites are characterized by shallow waters with quickly steepening slopes (Copping et al., 2018). In the Maldives, sightings also increase with slope. Areas of high zooplankton have been found in these areas, providing ideal foraging grounds (Sims, 2008, Eckert & Stewart, 2001). Distance from seamount was also a significant predictor of shark sightings; areas closer to seamounts had higher sightings. Afonso also found a link between abundance and seamounts (2014), finding more highly productive foraging areas in their vicinity. Dolphinsin the Maldives also associate with seamounts (Anderson et al., 1995). Bathymetry was only slightly significant in this study (p=0.05), however this may be due to all Maldives atolls having largely shallow depths.

Access to food resources can be driven by topographic conditions, and chl-a had a positive relationship to sightings. Monsoonally, whale sharks shift with changes in chlorophyll, moving between atolls to areas of higher chlorophyll content. Trophic links between chl-a and zooplankton are not immediate, yet similar relationships of sharks with chl-a have been found before (Sleeman et al., 2010., Kumari & Raman, 2010) as chl-a is the key driver of the phytoplankton-zooplankton-baitfish food chain (Rowat & Brooks, 2012). Tuna also associate with these blooms (Kumari, 2009); and multiple studies use tuna fisheries data to estimate whale shark occurrence (Sequira et al., 2012, Rowat, 2007). Whale sharks also show longer residencies in areas of higher chlorophyll content (Hsu, 2007). SST had a positive effect on shark sightings per month, and is an important driver in aggregations of whale sharks elsewhere and the most important in explaining habitat suitability in the Indian Ocean (Sequira et al., 2014).

Atoll was a significant predictor in sightings of moving sharks. Highest sightings occurred at Ari, with 43 out of the 47 moving sharks sighted in this atoll at some point. Ari is an aggregation site for sharks (Riley et al., 2010, Cagua et al., 2014, Copping et al., 2018), and therefore this result is not surprising. The significance of atoll as a predictor (accounting for 39.1% of variance) implies that sharks use different atolls seasonally. Linking atolls, seamounts and movement, fish assemblages at seamounts change seasonally (Jorgensen et al., 2016). Therefore movement could be driven by changes in prey abundance at these features, where seamounts of different atolls become more or less productive. To validate this, surveys of zooplankton are needed.

A positive DMI had a negative effect on sightings of moving sharks. Strong positive Indian Ocean Dipole result in negative SST anomalies. This could be due to a disruption in the monsoonal currents and thus upwelling in the area, as in certain dipole events, nutriclines can become deepened and thus penetration into the mixed layer is lost (Strutton et al., 2015). By combining sea surface height data and current data for the study period, greater rigour in this assumption can be given.

4.2 Seasonal

Whale sharks are seen in different atolls in different monsoons. First hypothesised by Anderson and Ahmad, 1993, this study is the first to evidently prove this. During the Southwest monsoon, sharks are found more regularly in Northern atolls. Davies (2014) found that *R.typus* visit the Northern atolls in the southwest monsoon to feed on the large masses of krill that bloom in this period. However, the reverse occurs in the Northeast monsoon, with shark sightings shifting to southern atolls, and sightings being recorded on the Eastern sides of atolls. This is likely due to a shift in food availability. Skipjack tuna (that feed on similar prey) have been found to show the same movement seasonally in the Maldives, migrating south in the northeast monsoon (Shiham Adam, 2002). Drifting objects, including plankton, are carried to the east coast in the northeast monsoon, therefore hypothetically bringing whale shark prey to the area (Anderson et al., 1996). The converse is true of the Southwest monsoon and therefore this explains the sightings in western Ari.

The temporal set in the GAMs explained 21.1% of variance again suggesting significant seasonal movement. This was particularly true of Baa, with sharks moving from South Ari around July to October to Baa and then moving back to Ari after this period. These were the most prolific (17 sharks showing movement; 3 of these sharks exhibited the same movement for 3 consecutive years). Specifically, a number of sharks entered Hanifaru Bay. The monsoonal and opposing tidal currents funnel and trap copepod rich plankton biomass into narrow Hanifaru Bay. This provides rich feeding grounds for plankton-feeding sharks and mantas (Brooks & Stevens, 2010). Further, in October and March, following periods of reduced winds and currents in the intermonsoon periods, Kitchen-Wheeler observed that spawning events of marine species often followed full moons (2013). Whale sharks have associated with spawning events in Christmas island (Hobbs et al., 2009) and Belize (Heyman et al., 2001), and therefore a link between movement and spawning events can be assumed for sharks moving to Baa. If spawn follows the same pattern of plankton biomass, spawning mass may get trapped in Hanifaru providing a very dense plethora of food. Furthermore, large densities of giant yellowfin tuna amass at Baa atoll in the southwest monsoon, signifying presence of feeding a possible event (Ahmad and Anderson, 1996). The sharks that exhibited movement between Baa and Thaa also showed this seasonal movement, with sharks sighted in Baa in the southwest monsoon and then in Thaa in the northeast. Sightings of sharks in Thaa were mostly composed of incidental sightings from bait fishermen, again increasing the hypothesis that sharks move for food.

Northward movement in the southwest monsoon (to Baa) and movements to Thaa and Gaafu in northeast monsoons show characteristic seasonal movements. Seasonal movement has been well documented in other whale shark movement studies (Macena et al., 2016., Taylor, 1996., Graham and Roberts, 2007). Baitfish distribution, a key zooplankton species, is influenced by the monsoons. Movements of damselfish, silversides and fusiliers exhibit the same movement that whale sharks do between monsoons; common southerly & easterly in the northeast and northerly and westerly in the southwest (Anderson, n.d.).

4.3 Limitations

While this study found evidence of whale shark movements and identified certain drivers of them, it comes with its limitations. Despite Maldives whale sharks receiving direct research attention from MWSRP, opportunistic and incidental sightings records remain the primary source of information for some atolls. These different sampling techniques led to a huge sampling bias that was impossible to account for in modelling, with Ari being overwhelmingly the most sampled atoll.

Secondly, there are limitations to relying on sightings data to assess movement. A shark not being sighted does not necessarily mean it is absent, or has exhibited movement. To fuel this, only 16% of sharks in South Ari (pers.comm) display signs of feeding at the surface, suggesting a lot of feeding occurs at depth and thus sharks may indeed be present during an apparent absence. In order to identify true movement, satellite tagging techniques should be deployed to back up the results from this study.

Many of the sharks recorded in the database were only seen once. {ast studies on mantas in the Maldives found a strong correlation between number of mantas re-sighted and number of surveys conducted, suggesting that with more surveys more mantas are re-sighted (Kitchen-Wheeler, 2013). It is highly likelt that the same be true of this dataset, as mantas and whale sharks prey on similar food (Rohner et al., 2013). Nonetheless, in Ari, an atoll that is well studied, only 62% of the individuals were ever re-sighted and so this bias may not be as significant as once thought.

4.4 Conclusions

The Maldives is home to a significant aggregation of whale sharks. This study was the first to look at movement on a country wide scale through sightings. It found that whale sharks move regularly within the Maldives, showing bi-annual movement between atolls linked with the monsoons. Sharks move South in the Northeast monsoon, and North in the Southwest. Secondly, sharks exhibit repeat movements (multi-year), exhibiting emigration and re-immigration. Through analysis of sightings against predictor variables, it was found that bathymetric features were the most important in determining whale shark presence, followed by temporal aspects. The environmental variables utilised within this study were only slightly significant to whale shark distribution. Utilisation of SLA and currents may provide some more insights into this highly seasonal movement found within the Maldives.

Further research is urgently needed to assess true movements. Although incidental sightings and CS has explored far greater areas than ever before, it is difficult to assess specific causes of movement from this data. Use of satellite tagging will be able to identify and confirm specific causes of movement, and also assess vertical movements that sightings data cannot.

Through applying these techniques, movement can be confirmed and important management measures put in place to protect sharks that deviate from South Ari’s protected waters to those that are unprotected.

References

Acuña-Marrero, D., Jiménez, J., Smith, F., Doherty, P., Hearn, A., Green, J., Paredes-Jarrín, J. and 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.

Adam, M.S. and Anderson, R.C., 1996. Yellowfin tuna (Thunnus albacares) in the Maldives. *The Maldivian Tuna Fishery: A collection of Tuna Resource Research Papers, Maldives Marine Research Bulletin*, *2*, pp.23-39.

Afonso, P., McGinty, N. and Machete, M. (2014). Dynamics of Whale Shark Occurrence at Their Fringe Oceanic Habitat. *PLOS ONE*, 9(7).

Anderson, C. (n.d.). The Maldivian Tuna Livebait Fishery - Status and Trends. *Marine Research Section, Ministry of Fisheries and Agriculture Malé, Republic of Maldives*.

Anderson, C., Branch, T.A., Alagiyawadu, A.N.O.M.A., Baldwin, R. and Marsac, F., 2012. Seasonal distribution, movements and taxonomic status of blue whales (Balaenoptera musculus) in the northern Indian Ocean. *Journal of Cetacean Resources and Management*, *12*(2), pp.203-218.

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.

Anderson, R.C., 1996. First records of Fraser’s dolphin (Lagenodelphis hosei) from the Maldives. *J. South Asian Nat. Hist*, *2*, pp.75-80.

Andrzejaczek, S., Meeuwig, J., Rowat, D., Pierce, S., Davies, T., Fisher, R. and Meekan, M. (2016). The ecological connectivity of whale shark aggregations in the Indian Ocean: a photo-identification approach. *Royal Society Open Science*, 3(11), p.160455.

Bean, B. (1902). A rare 'whale shark.'. *Science*, 15(374), pp.353-353.

Bennett, G. (1834). *Wandering in New South Wales, Batavia, Pedir Coast, Singapore and China. Vol. II.*. 1st ed. London, pp.267-280.

Betzler, C., Fürstenau, J., Lüdmann, T., Hübscher, C., Lindhorst, S., Paul, A., Reijmer, J. and Droxler, A. (2012). Sea-level and ocean-current control on carbonate-platform growth, Maldives, Indian Ocean. *Basin Research*, 25(2), pp.172-196.

Bradshaw, C., Fitzpatrick, B., Steinberg, C., Brook, B. and Meekan, M. (2008). Decline in whale shark size and abundance at Ningaloo Reef over the past decade: The world's largest fish is getting smaller. *Biological Conservation*, 141(7), pp.1894-1905.

Brooks, K., & Stevens, G. (2010). Developing Tourism at Hanifaru Bay Marine Protected Area (MPA) – Report for Maldivian Government (pp. 1-12).

Brunnschweiler, J., Baensch, H., Pierce, S. and Sims, D. (2009). Deep-diving behaviour of a whale sharkRhincodon typusduring long-distance movement in the western Indian Ocean. *Journal of Fish Biology*, 74(3), pp.706-714.

Burnham, K., Anderson, D. and Huyvaert, K. (2010). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65(1), pp.23-35.

Cagua, E.F., Collins, N., Hancock, J. and Rees, R., 2014. Whale shark economics: a valuation of wildlife tourism in South Ari Atoll, Maldives. *PeerJ*, *2*, p.e515.

Compagno, L.J.V., 2001. Sharks of the world: an annotated and illustrated catalogue of shark species know to date. FAO Species Catalogue for Fishery Purposes, No. 1, vol. 2. Bullhead, Mackerel and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes). U.N. Dev. Prog, Rome, 269 pp.

Copping, J., Stewart, B., McClean, C., Hancock, J. and Rees, R. (2018). Does bathymetry drive coastal whale shark (Rhincodon typus) aggregations?. *PeerJ*, 6, p.e4904.

Davies, T. (2014). Social Media Monitors the Largest Fish in the Sea. *American Scientist*, 102(2), p.116.

Diamant, S., Rohner, C., Kiszka, J., Guillemain d'Echon, A., Guillemain d'Echon, T., Sourisseau, E. and Pierce, S. (2018). Movements and habitat use of satellite-tagged whale sharks off western Madagascar. *Endangered Species Research*, 36, pp.49-58.

Donati G, Rees RG, Hancock JW, Jenkins TK, Shameel I, Hindle K, Zareer I, Childs A, Cagua EF. New insights into the South Ari atoll whale shark, Rhincodon typus, aggregation. QScience Proceedings (The 4th International Whale Shark Conference) 2016:iwsc4.16 http://dx.doi.org/10.5339/qproc.2016.iwsc4.16

Dudgeon, C. and White, W. (2012). First record of potential Batesian mimicry in an elasmobranch: juvenile zebra sharks mimic banded sea snakes?. *Marine and Freshwater Research*, 63(6), p.545.

Eckert, S.A. and Stewart, B.S., 2001. Telemetry and satellite tracking of whale sharks, Rhincodon typus, in the Sea of Cortez, Mexico, and the north Pacific Ocean.

In *The behavior and sensory biology of elasmobranch fishes: an anthology in memory of Donald Richard Nelson* (pp. 299-308). Springer, Dordrecht.

GEBCO. 2018 General bathymetric chart of the oceans. Available at http://www.gebco.net.

Gifford, A., Compagno, L., Levine, M. and Antoniou, A. (2007). Satellite tracking of whale sharks using tethered tags. *Fisheries Research*, 84(1), pp.17-24.

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

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

Hueter, R., Tyminski, J. and de la Parra, R. (2013). Horizontal Movements, Migration Patterns, and Population Structure of Whale Sharks in the Gulf of Mexico and Northwestern Caribbean Sea. *PLoS ONE*, 8(8), p.e71883.

Jorgensen, S., Klimley, A., Muhlia-Melo, A. and Morgan, S. (2016). Seasonal changes in fish assemblage structure at a shallow seamount in the Gulf of California. *PeerJ*, 4, p.e2357.

Kitchen-Wheeler, A., Ari, C. and Edwards, A. (2011). Population estimates of Alfred mantas (Manta alfredi) in central Maldives atolls: North Male, Ari and Baa. *Environmental Biology of Fishes*, 93(4), pp.557-575.

Kitchen-Wheeler, AM. (2013). *The behaviour and ecology of Alfred mantas (Manta Alfredi) in the Maldives*. PhD thesis. Newcastle University. *http://hdl.handle.net/10443/1936*

Kitchingman, A. and S. Lai. 2004. “Inferences on potential seamount locations from mid-resolution bathymetric data.” In: Morato T, Pauly D (eds) Seamounts: Biodiversity and Fisheries. Fisheries Centre, University of British Colombia, Vancouver, Canada, pp 7-12

Kumari, B. & Raman, M. (2010) Whale shark habitat assessments in the northeastern Arabian Sea using satellite remote sensing. International Journal of Remote Sensing, 31, 379–389

Kumari, B., Raman, M. & Mali, K. (2009). Locating tuna forage ground through satellite remote sensing. *International Journal of Remote Sensing* 30, 5977–5988

Lüdmann, T., Kalvelage, C., Betzler, C., Fürstenau, J. and Hübscher, C. (2013). The Maldives, a giant isolated carbonate platform dominated by bottom currents. *Marine and Petroleum Geology*, 43, pp.326-340.

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).

Marliana, S., Bataona, M. and Ihsan, E. (2018). Zooplankton communities in Cenderawasih Bay National Park, West Papua: can their composition be used to predict whale shark Rhincodon typus Smith, 1828 appearance frequencies?. IOP Conference Series: Earth and Environmental Science, 139, p.012012.

McKinney J, Hoffmayer ER, Holmberg J, Graham R, de la Parra R et al. (2013) Regional connectivity of whale sharks demonstrated using photo-identification - Western Atlantic, 1999 - 2013. PeerJ PrePrints 1:e98v1

McKinney, J., Hoffmayer, E., Holmberg, J., Graham, R., Driggers, W., de la Parra-Venegas, R., Galván-Pastoriza, B., Fox, S., Pierce, S. and Dove, A. (2017). Long-term assessment of whale shark population demography and connectivity using photo-identification in the Western Atlantic Ocean. *PLOS ONE*, 12(8), p.e0180495.

McKinney, J., Hoffmayer, E., Wu, W., Fulford, R. and 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.

NASA, 2018. Ocean Color Data Available at: https://oceancolor.gsfc.nasa.gov/

Pierce, S, and Norman, B. 2016. Rhincodon typus. The IUCN Red List of Threatened Species 2016: e.T19488A2365291.

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

Riley, M., Harman, A. and Rees, R. (2009). Evidence of continued hunting of whale sharks Rhincodon typus in the Maldives. *Environmental Biology of Fishes*, 86(3), pp.371-374.

Robinson, D., Jaidah, M., Bach, S., Rohner, C., Jabado, R., Ormond, R. and Pierce, S. (2017). Some like it hot: Repeat migration and residency of whale sharks within an extreme natural environment. *PLOS ONE*, 12(9), p.e0185360.

Rohner, C., Armstrong, A., Pierce, S., Prebble, C., Cagua, E., Cochran, J., Berumen, M. and Richardson, A. (2015). Whale sharks target dense prey patches of sergestid shrimp off Tanzania. Journal of Plankton Research, 37(2), pp.352-362.

Rohner, C., Pierce, S., Marshall, A., Weeks, S., Bennett, M. and 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. (2007). Occurrence of whale shark (Rhincodon typus) in the Indian Ocean: A case for regional conservation. *Fisheries Research*, 84(1), pp.96-101.

Rowat, D. and Brooks, K. (2012). A review of the biology, fisheries and conservation of the whale shark Rhincodon typus. *Journal of Fish Biology*, 80(5), pp.1019-1056.

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.

Ryan, J., Green, J., Espinoza, E. and Hearn, A. (2017). Association of whale sharks (Rhincodon typus) with thermo-biological frontal systems of the eastern tropical Pacific. *PLOS ONE*, 12(8), p.e0182599.

Saji, NH., Yamagata, T. Possible impacts of Indian Ocean Dipole mode events on global climate. T, CLIMATE RES, 25 (2): 151-169 DEC 5 2003.

Sandulli, R., Semprucci, F. and Balsamo, M. (2014). Taxonomic and functional biodiversity variations of meiobenthic and nematode assemblages across an extreme environment: a study case in a Blue Hole cave. *Italian Journal of Zoology*, 81(4), pp.508-516.

Sasamal, S. (2007). Island wake circulation off Maldives during boreal winter, as visualised with MODIS derived chlorophyll-adata and other satellite measurements. *International Journal of Remote Sensing*, 28(5), pp.891-903.

Sequeira A, Mellin C, Rowat D, Meekan MG, Bradshaw CJA. 2012. Ocean-scale prediction of whale shark distribution. Diversity Distrib.18, 504–518. (doi:10.1111/j.1472-4642.2011.00853.x)

Sequeira, A., Mellin, C., Floch, L., Williams, P. and Bradshaw, C. (2014). Inter-ocean asynchrony in whale shark occurrence patterns. *Journal of Experimental Marine Biology and Ecology*, 450, pp.21-29.

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 Distribution* 18: pp504–518.

Sequeria AMM, Mellin C, Meekan MG, Sims DW, Bradshaw CJA. 2013 Inferred global connectivity of whale shark Rhincodon typu spopulations. J. Fish. Biol. 82, 367–389. (doi:10.1111/jfb.12017) 26.

Shiham Adam, M. (2002). Population dynamics and movements of skipjack tuna (Katsuwonus pelamis) in the Maldivian fishery: analysis of tagging data from an advection-diffusion-reaction model. *Aquatic Living Resources*, 15(1), pp.13-23.

Sims, D. (2008). Chapter 3 Sieving a Living. *Advances in Marine Biology*, pp.171-220.

Sleeman, J., Meekan, M., Fitzpatrick, B., Steinberg, C., Ancel, R. and Bradshaw, C. (2010). 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. and Bradshaw, C. (2010). 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.

Strutton, P., Coles, V., Hood, R., Matear, R., McPhaden, M. and Phillips, H. (2015). Biogeochemical variability in the central equatorial Indian Ocean during the monsoon transition. *Biogeosciences*, 12(8), pp.2367-2382.

Taylor JG, Pearce AF (1999) Ningaloo Reef currents: impli- cations for coral spawn dispersal, zooplankton and whale shark abundance. J R Soc West Aust 82:57–65

Thomson, J., Araujo, G., Labaja, J., McCoy, E., Murray, R. and Ponzo, A. (2017). Feeding the world's largest fish: highly variable whale shark residency patterns at a provisioning site in the Philippines. *Royal Society Open Science*, 4(9), p.170394.

Turnbull, S. and Randell, J. (2006). Rare Occurrence of a Rhincodon typus (Whale Shark) in the Bay of Fundy, Canada. *Northeastern Naturalist*, 13(1), pp.57-58.

Tyminski, J., de la Parra-Venegas, R., González Cano, J. and 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.

Wilson SG, Taylor JG, Pearce AF (2001) The seasonal aggrega- tion of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Niño/ Southern Oscillation. Environ Biol Fish 61:1–11