

Does Bathymetry Drive Whale Shark Aggregations?

Joshua Copping (Y3840781)

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Supervised by Bryce Beukers-Stewart & Colin McClean

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Abstract

Whale sharks, *Rhincodon typus*, form seasonal feeding aggregations in coastal waters around the world. Most research has studied individual aggregations and prey availability, without investigating factors known to influence other megafauna aggregations. A number of studies have shown the basking shark and megamouth shark, are more abundant in areas with bathymetric features known to cause higher primary productivity. Therefore, this study examines the bathymetry in areas *R. typus* aggregation events occur, with the aim to understand whether bathymetry influences aggregations. The research carried out shows there are similarities in bathymetry between aggregation sites, significantly different from other coastal areas within *R. typus*' global range. Evidence shows aggregations occur in areas with specific bathymetric features; shallow coastal areas in close proximity to water in the mesopelagic zone, connected by steep gradient slopes such as reef slopes or continental shelf breaks. These factors are known to induce upwelling events, increasing primary productivity, consequently attracting a number of filter feeding species. This study has shown bathymetry does influence *Rhincodon typus* aggregations and has filled in knowledge gaps missing from previous research.

1 Introduction

1.1 Marine megafauna

Marine ecosystems are among the most threatened areas on earth (MEA, 2005; Halpern *et al.*, 2007). Both habitats and the species inhabiting them face a growing number of threats caused by climate change; ocean warming and acidification and increasing rates of overexploitation and incidental capture in the fisheries industry (Halpern *et al.*, 2007; Hoegh-Guldberg and Bruno, 2010). Such threats often exhibit disproportionate impacts on marine megafauna; Read *et al.*, (2006) show up to 70% of cetaceans in the US have been entangled in fishing gear at least once in their life and Abercrombie *et al.*, (2005) found shark bycatch contributed to over 25% of the catch in US pelagic longline fisheries between 1992 and 2003. Even when exploitation has ended, it can still have substantial negative impacts on the size and recruitment rate of populations. Whitehead *et al.*, (2005) discovered the Galapagos Islands sperm whale (*Physeter macrocephalus*) population declined by a rate of 20% per year between 1985-1995, despite no hunting in the area since 1981.

The consequences of marine megafauna exploitation and subsequent declines are far reaching; marine megafauna are often apex predators, therefore their removal has cascading impacts on lower trophic levels, causing community restructuring and enhanced vulnerability of other species (Myers *et al.*, 2007). Impacts are not only ecological; presence of megafauna often contributes to local economies significantly

through ecotourism (Catlin and Jones, 2010). Regardless of their importance, little is understood about the factors affecting the movements and global distributions of many marine megafauna species. Identifying and understanding areas used in important periods of their life is essential for future conservation efforts (Hooker *et al.*, 1999). The whale shark (*Rhincodon typus*) is one species where little information is known about their global distribution, movements and the factors affecting these. This study aims to address this, by focusing on the factors impacting *R. typus* feeding aggregations.

1.2 Whale sharks

Rhincodon typus is one of three large pelagic filter feeding shark species and is the largest fish in the world (Stevens, 2007). They have a circumglobal distribution, found in all tropical and warm temperate seas except the Mediterranean, with their typical range between the latitudes of 30°N and 35°S (Castro *et al.*, 2007). As filter feeders, *Rhincodon typus* primarily feed on zooplankton, therefore tend to be observed in areas with high productivity (Colman, 1997). However, recent studies have shown whale sharks also feed on a variety of coral, fish and invertebrate spawn (Stevens, 2007). There is no robust population estimation for this species, which is listed as vulnerable on the IUCN Red List (Norman, 2005). Although, their late sexual maturation, highly migratory nature and low abundance make this species extremely vulnerable, particularly to incidental capture and overexploitation that has

caused global population decline and fragmentation (Dulvy *et al.*, 2008). More recently, the economic value of live whale sharks to ecotourism has been shown to be considerably higher than when fished (Catlin and Jones, 2010).

The importance of this species, ecologically and economically has triggered a growing interest amongst the scientific community, with the majority of papers on *Rhincodon typus* published within the past two decades. Together with the increases in ecotourism, there is now a great depth of knowledge into local and regional whale shark ecology and biology (Rowat and Brooks, 2012). Yet there is still a dearth of information in global distribution, especially connectivity of populations and migratory patterns (Sequeira *et al.*, 2012). *Rhincodon typus* were once perceived to be solitary animals that live and feed in the open ocean, however the increasing volume of literature now shows they are a gregarious species, often observed in seasonal feeding aggregations (Colman, 1997; Heyman *et al.*, 2001; Riley *et al.*, 2010).

1.3 *Rhincodon typus* aggregations

Research shows there could be as many as 20 *Rhincodon typus* aggregation areas around the world (Castro *et al.*, 2007; Stevens, 2007; Graham and Roberts, 2007). Although literature regarding aggregations varies considerably as certain sites have been studied extensively, such as Ningaloo Reef in Western Australia, perhaps the most famous aggregation (Wilson *et al.*, 2001). There is great variability among

aggregation events in terms of available prey, when they occur and the number of individuals aggregating (Heyman *et al.*, 2001). Studies have shown *R. typus* aggregate in areas of high biological productivity and the seasonal nature of such aggregations appears to be the result of local increases in prey (Meekan *et al.*, 2006; Rowat *et al.*, 2007; Rowat *et al.*, 2009). The co-occurrence of aggregation events and increased prey availability in a number of locations allows aggregations to be highly predictable. For example, whale sharks are not regularly seen at Gladden Spit, Belize, until full moon periods in April and May each year where a large number aggregate to feed on the spawn of snappers (Lutjanidae spp.) (Heyman *et al.*, 2001). This is again reflected in the Gulf of Tadjouran, Djibouti when throughout the winter months (November to February) a large aggregation of *R. typus* can be observed feeding on zooplankton (Rowat *et al.*, 2007).

One of the main observed differences between aggregations is the number of *R. typus* at each site; aggregations can contain around 10 to 20 individuals such as at Gladden Spit or Donsol Bay in the Philippines (Quiros, 2007), or as many as several hundred individuals which have been observed in extremely plankton rich areas such as recently discovered “Afuera” aggregation off the Mexican coast (de la Parra Venegas *et al.*, 2011). Another difference between aggregation sites is the spatial segregation of *R. typus* by size and gender, which is typical in shark populations (Springer, 1967). Observations from most *R. typus* aggregations show populations dominated by juvenile males (Heyman *et al.*, 2001; Meekan *et al.*, 2006; Rowat *et*

al., 2007), which are thought to be part of a larger population not observed by current research by remaining in deeper areas where aerial and boat based observations cannot investigate (Brunnschweiler *et al.*, 2009).

R. typus is a pelagic species believed to spend most of their lives in deep offshore waters apart from during seasonal aggregations (Stevens, 2007). There have only been a handful of studies researching the deep diving behaviour of *R. typus*, nonetheless they suggest *R. typus* dives to the mesopelagic zone to feed. Graham *et al.*, showed this in 2006 using pop-up archival satellite tags, which recorded one individual diving to a depth of 979.5 m at the Mesoamerican Barrier Reef, Belize. Using similar equipment, Brunnschweiler *et al.*, (2009) recorded *R. typus* diving to depths of 1,264m in the Mozambique Basin. Both studies indicate deep water is important for *R. typus*, therefore the underlying bathymetry could play a role in aggregation events.

1.4 What is bathymetry?

The depth of the seafloor, gradient of slopes and underwater features are known as bathymetry or submarine topography. Bathymetric features such as continental and reef slopes, shallow banks and seamounts tend to be areas of high marine productivity, in particular high zooplankton abundance, often driving predator prey aggregations (Yen *et al.*, 2004). Bouchet *et al.*, (2015), show areas with complex

bathymetry such as seamounts or steep gradients found on outer reefs, accumulate zooplankton and subsequently attracts filter feeders, particularly at epipelagic and mesopelagic depths. Sims, (2008) show the basking shark *Cetorhinus maximus*, are more abundant in areas with steeper, owed to the higher densities of zooplankton.

Studies have shown almost all *R. typus* aggregations occur in area of shallow bathymetry in close proximity to the reef slope and deeper water (Castro *et al.*, 2007; Stevens, 2007). Past studies have illustrated increased zooplankton availability in areas of steep bathymetry, which *R. typus* preys upon (Bouchet *et al.*, 2015). Therefore, bathymetry at and around areas of aggregation events could be an important factor in driving them. There are currently no studies into bathymetry and *Rhincodon typus*, this lack of information could be detrimental to the future conservation of this species (Rowat and Brooks, 2012).

1.5 Aim and objectives

The aim of this study is to investigate whether bathymetry influences *Rhincodon typus* aggregations by looking at a number of factors deemed important in current literature. To meet the aim, the following questions will be answered:

- I. Are there similarities in bathymetry between aggregation sites?
- II. How does this compare to bathymetry at non-aggregation sites?

- III. Which bathymetric variable has the biggest influence on aggregations?
- IV. What is the biggest driver of aggregations?

2 Methods

2.1 Data acquisition

To identify *R. typus* aggregation sites an extensive literature review was carried out using the following search terms in Web of Science and Google Scholar: Whale shark, *Rhincodon typus*, aggregation, bathymetry, topography, relief, depth, movements, feeding. Upon finding a large number of sources, all articles were evaluated and papers that mentioned aggregations retained for further use. A database of 15 aggregation events (Table 2.1) was created containing size, spatial and temporal occurrence and coordinates at the centre of the aggregation. Although more sites were found in the literature, there was insufficient information to include them in this study.

Table 2.1. Summary of the aggregation site names and locations used in this study with the literature sources where information has been extracted. Sites marked with ‘*’ indicate they were later removed from analysis, explained in subsequent sections.

Aggregation location	Sources
Australia, Ningaloo Reef	Taylor, 1996; Wilson <i>et al.</i> , 2001; Meekan <i>et al.</i> , 2006; Catlin & Jones, 2010
Belize, Gladden Spit	Heyman <i>et al.</i> , 2001; Graham <i>et al.</i> , 2006; Quiros, 2007
*Christmas Island, West Coast	Hobbs <i>et al.</i> , 2009; Meekan <i>et al.</i> , 2009
Djibouti, Gulf of Tadjoura	Rowat <i>et al.</i> , 2007; Schmidt <i>et al.</i> , 2009; Rowat <i>et al.</i> , 2012
Gulf of California, La Paz	Eckert & Stewart, 2001; Nelson & Eckert, 2007; Stevens, 2007
*Gulf of Mexico, North Area	Hoffmayer <i>et al.</i> , 2007; McKinney <i>et al.</i> , 2012
Madagascar, Nosy Be	Jonahson & Harding, 2007; Brunnschweiler <i>et al.</i> , 2009
Maldives, South Ari Atoll	Riley <i>et al.</i> , 2009; Riley <i>et al.</i> , 2010
Mexico, Afuera	de la Parra Venegas <i>et al.</i> , 2011; Hueter <i>et al.</i> , 2013
Mexico, Yucatan Peninsula	Motta <i>et al.</i> , 2010; Ziegler <i>et al.</i> , 2012; Hueter <i>et al.</i> , 2013
Mozambique, Tofo Beach	Brunnschweiler <i>et al.</i> , 2009; Sequeira <i>et al.</i> , 2012
Philippines, Donsol Bay	Eckert <i>et al.</i> , 2002; Quiros, 2007
*Qatar, Al-Shaheen Oil Field	Moore, 2012; Robinson <i>et al.</i> , 2013
Saudi Arabia, Al-Lith	de la Torre <i>et al.</i> , 2012; Berumen <i>et al.</i> , 2014

A shapefile of *R. typus* global range was obtained from the IUCN (IUCN, 2005) to examine the spatial distribution of aggregation sites. Bathymetric depth data was obtained from the General Bathymetric Chart of the Oceans (GEBCO); the 2014 30 arc-second global grid at a resolution of 1km was downloaded (GEBCO, 2015) as seven tiles spanning *R. typus*' range. Environmental factors were obtained from OceanColor (NASA, 2014), an archive of oceanographic data from satellite based remote sensing. Sea surface temperature (SST) data was downloaded as a seasonal composite of the years 2000 to 2016 at a 4km resolution recorded by the Terra MODIS instrument. A seasonal composite of chlorophyll-a concentration from

2012 to 2016 at a 4km resolution, recorded by the SNPP-VIIRS instrument was also downloaded. Seasonal composites were used as *R. typus* aggregate seasonally and a composite of a number of years should mitigate the influence of anomalies such as El Niño. This data was selected as it is the most current data available.

2.2 Spatial analysis

The seven bathymetry tiles were opened in ArcMap, merged and had all data with an elevation greater than sea level removed. Chlorophyll and SST data were imported and resampled to a 1km resolution for comparison with bathymetry data. Using the spatial analysis toolbox, slope and curvature layers were generated from bathymetric depth to examine gradient and shape of features. Curvature layer assign a value to each pixel dependent upon the shape; positive values indicate upwardly concave slopes and negative values show upwardly convex slopes, values close to 0 indicate planar slopes.

Rhincodon typus aggregation point data was imported and locations checked using imagery basemaps and source papers to ensure locations were correct. To compare aggregation sites to areas aggregations do not occur, 1,000 random absence points were created (Figure 2.1). Random points were constrained to coastal areas in the global range of *R. typus* by calculating the maximum distance of aggregation sites from the coast and using this figure to create a buffer zone around coastlines within

R. typus range. Although *R. typus* has a global range, literature shows aggregations only occur in coastal zones, therefore unproductive and deep high seas areas were excluded as this would skew the data.

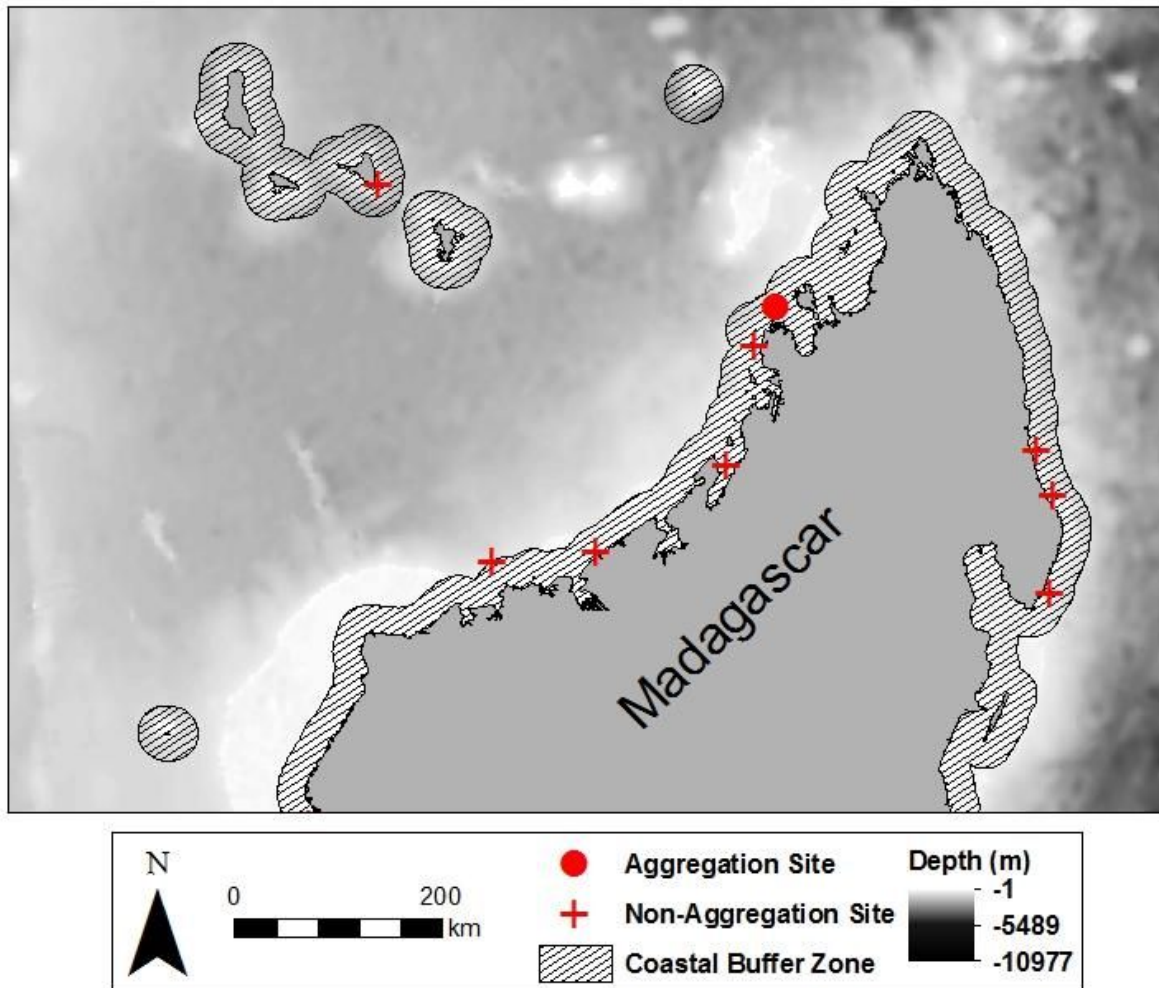


Figure 2.1. A map showing the coastal buffer zone around Madagascar used to constrain the 1,000 random non-aggregation site points also shown in the map, along with the Madagascar aggregation site at Nosy Be Island and the background basic bathymetric depth data.

20km buffer zones were generated around each aggregation and random point, allowing extraction of information about the surrounding areas. Using the zonal statistics tool; minimum, maximum, mean, range and standard deviation were extracted for depth, gradient and slope curvature for the point data and buffer zones. SST and chlorophyll data was extracted by the same method but only for point data, not buffer zones as these factors are considered important only in the area of aggregation (Stevens, 2007). Proximity analysis was performed on points, measuring distance to 200m and 1,000m deep water (mesopelagic and bathypelagic zones) shown to be important for *R. typus* feeding (Brunnschweiler *et al.*, 2009). All data was tabulated for subsequent statistical analysis.

2.3 Statistical analysis

Although a range of statistics were extracted during spatial analysis, points only encompassed one grid cell due to the low-resolution bathymetry data, therefore not all measurements were used (Table 2.2.). While investigating the data, it was noted aggregations occurred during seasons with the highest chlorophyll-a concentration and SST, therefore maximum value across the four seasons was extracted for each and this figure was used. After importing data into R and checking for skew and heteroscedasticity, three of the aggregation sites (Christmas Island, Gulf of Mexico and Qatar) were removed from analysis due to high residual deviance and

appearance as outliers. Of the 1,000 points, five were in no data areas for a particular layer, so were removed, leaving 995 random points for analysis.

Basic statistics were run on the variables, examining means and variance. To test whether differences were significant an independent samples t-test was used. This was chosen due to its power and robustness particularly with large datasets (Zimmerman, 1987; Erceg-Hurn and Mirosevich, 2008). Generalised linear models (GLMs) with a binomial error function were used to investigate which variable had the greatest influence on aggregation presence. Whilst examining data, a number of predictor variables exhibited collinearity. To minimise this, four GLM's were created to separate collinear variables and subsequently contained predictor variables with no or weak correlation. The four model outputs showed no overdispersion so minimum adequate models were created using backward-forward stepwise reduction based on the Akaike Information Criterion (AIC) (Hilbe, 1994; Dobson and Barnett, 2008). To test whether the deviance explained had not reduced from the full models therefore justifying the use of stepwise reduction, analysis of deviance was used (McCulloch, 2000).

Table 2.2. Summary of the variables extracted from spatial analysis, the measurement of the variable and the name they were called in the GLM.

Variable	Measurement	Name
Mean point depth	Mean depth	Site depth
Mean buffer zone depth	Mean depth	Buffer depth
Max buffer zone depth	Maximum depth	Buffer max
Buffer zone depth range	Depth range	Depth range
Bathymetric complexity	Depth standard deviation	Complexity
Mean point gradient	Mean gradient	Site gradient
Mean buffer zone gradient	Mean gradient	Buffer gradient
Maximum buffer zone gradient	Maximum gradient	Max gradient
Curvature at point	Mean curvature	Site Curvature
Mean curvature in buffer zone	Mean curvature	Mean Curvature
Maximum curvature in buffer zone	Maximum curvature value	Concavity
Minimum curvature in buffer zone	Minimum curvature value	Convexity
Proximity to 200m	Distance to 200m isobath	200m
Proximity to 1,000m	Distance to 1,000m isobath	1000m
SST	Mean SST	SST
Chlorophyll-a concentration	Mean Chlorophyll-a concentration	Chlorophyll

3 Results

3.1 Depth

Across the 12 aggregation sites the mean site depth was 22.17m [95% confidence interval 16.08 – 28.83], whereas non-aggregation sites had a mean depth of 635.29m [574.29 – 697.90] (Figure 3.1a); an increase in depth of over 2700%. These differences were highly significant with a t-test ($t = 19.258$, $df = 1005$, $p = 2.2 \times 10^{-9}$).

Similarly, the differences between mean depth in the 20km buffer zones; 197.21m [107.76 – 301.79] for aggregation sites, and 713.56m [655.68 – 772.72] for non-aggregation sites were also shown to be highly significant ($t = 8.529$, $df = 19.5$, $p = 5.2 \times 10^{-8}$). The maximum depths in the 20km buffer zones were different for aggregation and non-aggregation sites (Figure 3.1b) with means of 818.08m [441.81 – 1255.42] and 1350.82 [1260.74 – 1442.92], these differences were significant ($t = 2.36$, $df = 11.99$, $p = 0.035$)

There were differences in the range of depths; aggregation sites had 63% less range compared to non-aggregation sites. The mean ranges were 814.17m [439.43 – 1255.27] and 1295.26m [1207.27 – 1385.36] respectively, with near significant differences in means. The standard deviation of depth, used as an indicator of bathymetric complexity showed greater mean complexity at non-aggregation sites; 336.52 [312.78 – 361.01] compared to aggregation sites with a mean of 206.82 [95.10 – 341.78]. These differences in bathymetric complexity show aggregation sites have a less undulating surface however it was not significantly different from non-aggregation sites.

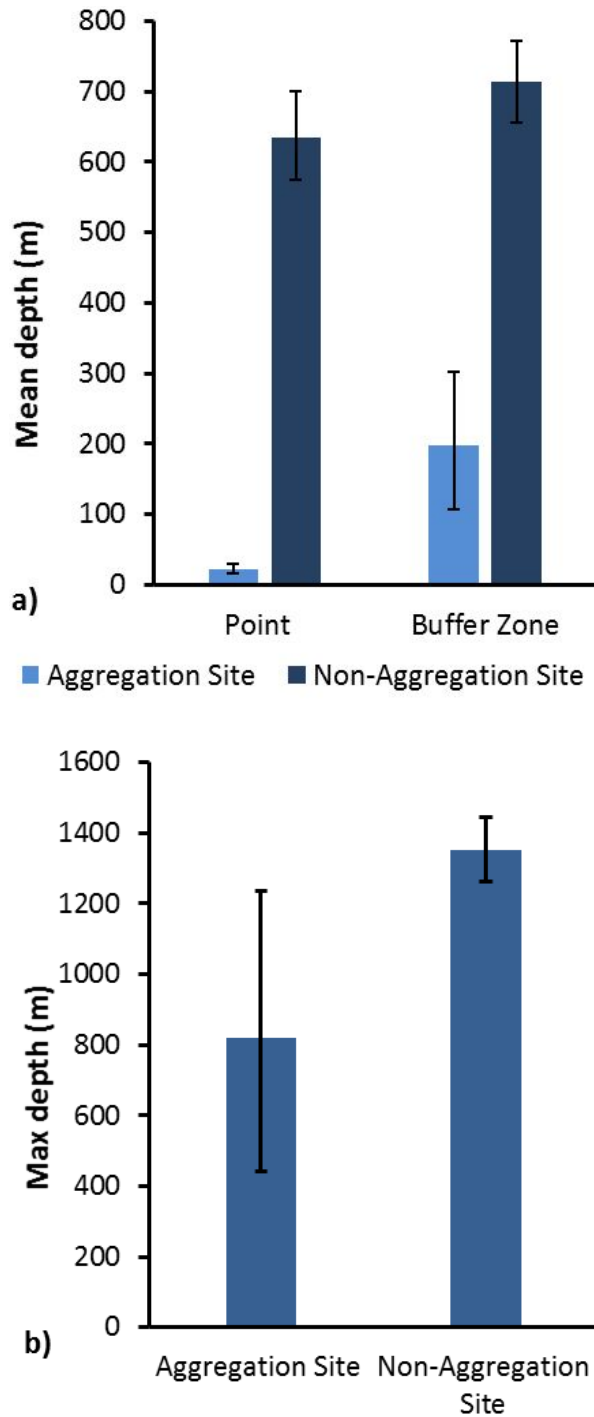


Figure 3.1. Graphs showing difference in depth variables between aggregation and non-aggregation sites. **a)** shows mean depth for point and buffer data. **b)** shows maximum depth for buffer data. Both graphs plotted with 95% confidence interval error bars.

3.2 Slope

Aggregation sites showed a significantly steeper mean gradient than non-aggregation sites; 0.77 degrees [0.33 – 1.3] and 0.00003 degrees [-0.0005 – 0.0006], ($t = 2.94$, $df = 11$, $p = 0.013$). However, mean gradient in buffer zones, showed the opposite, with the steeper gradient at non-aggregation sites 2.55 [2.38 – 2.73] instead of aggregation sites 1.60 degrees [0.85 – 2.40], which was shown to be significant ($t = 2.24$, $df = 12$, $p = 0.044$). t-tests showed no significant differences in mean maximum gradient; aggregation sites 9.60 degrees [5.34 – 14.63], similar to that at non-aggregation sites; 10.31 degrees [9.67 -10.96], although absolute maximum gradient recorded were steeper; aggregation sites 29.84 degrees, non-aggregation sites 60.15 degrees.

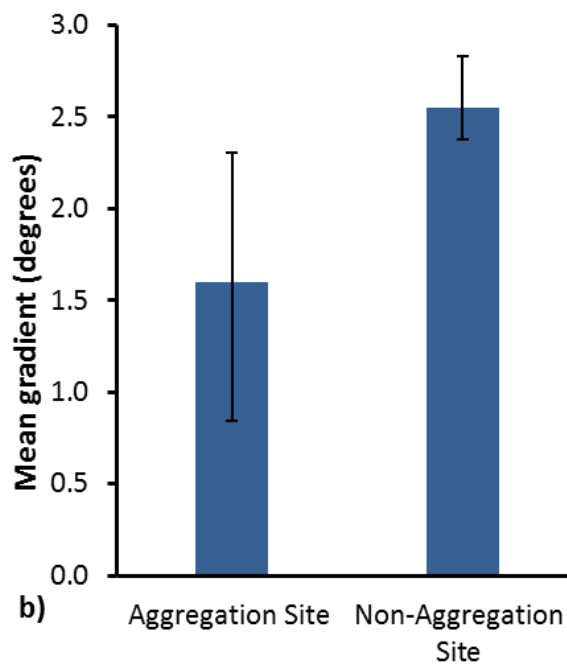
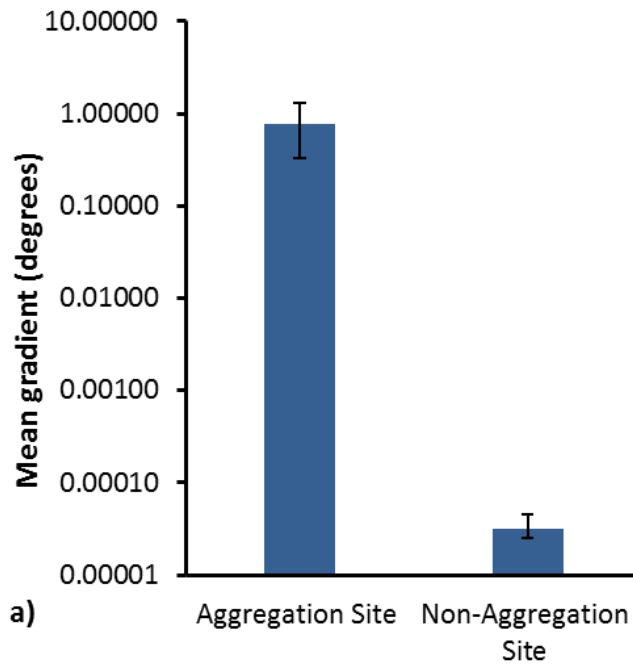


Figure 3.2. Graphs showing differences in mean gradient between aggregation sites and non-aggregation sites. **a)** shows mean at site gradient and **b)** shows mean buffer zone depth. Both plotted with 95% confidence interval error bars.

The shape of the slopes was concave at and around both aggregation and non-aggregation sites. However, non-aggregation sites were slightly more concave with a mean value of 1.08×10^{-5} , compared with 3.83×10^{-6} at aggregation sites. In contrast, the buffer zones around aggregation sites showed greater concavity than areas around non-aggregation sites with means of 3.66×10^{-6} and 2.63×10^{-6} respectively. The degree of slope concavity at aggregation sites was higher than non-aggregation sites; 0.00064 compared to 0.00058. Aggregation sites also exhibit greater convexity with a value of -0.00066, whereas non-aggregation sites had -0.00059. Despite differences in shape of slopes at and around aggregation and non-aggregation sites, none of these differences were significant.

3.3 Proximity to deeper water

Aggregation sites were 2 orders of magnitude closer to the 200m isobath with a mean distance of 0.14km [0.07 – 0.24], where the mean distance for non-aggregation sites was 71.78km [62.21 – 81.77]. Also reflected in the distance to the 1,000m isobath due to autocorrelation with the 200m depth variable. Aggregation sites had a mean distance of 0.41km [0.26 – 0.57] compared to non-aggregation sites which had a mean distance of 99.38km [88.70 – 110.62]. The observed differences in distance to both the 200m and 1,000m isobath were highly significant by the t-tests; ($t = 14.4$, $df = 994$, $p = 2.2 \times 10^{-9}$) for 200m and ($t = 17.6$, $df = 994$, $p = 2.1 \times 10^{-9}$) for the differences at 1,000m.

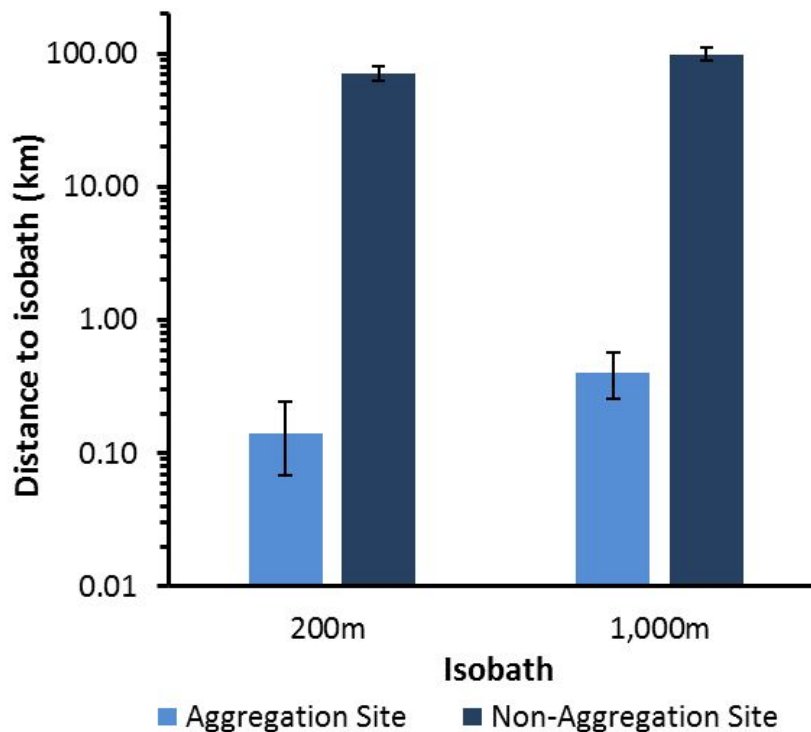


Figure 3.3. Mean distance (km) of aggregation and non-aggregation sites to the 200m and 1,000m isobaths plotted with a logarithmic y-axis and 95% confidence interval error bars.

3.4 Environmental factors

Although there were small differences in chlorophyll-a concentration and SST between aggregation and non-aggregation sites, neither were significant.

Chlorophyll-a was lower at aggregation sites with a mean concentration of 0.70mg/m^3 [0.50 – 0.95], whereas the mean chlorophyll-a concentration at non-aggregation sites was 1.53mg/m^3 [1.37 – 1.71]. SST showed the opposite, with a

mean of 30.26°C [29.74 – 30.71] at aggregation sites, compared to 29.80°C [29.58 – 30.00] at non-aggregation sites.

3.5 Main drivers of aggregations

The six predictor variables left in the four minimum adequate models were significant ($p < 0.05$) and three of the models (Table 3.1) had high percentage of deviance explained for aggregation site presence. Aggregation site presence was best modelled by GLM3, with the mean depth in the buffer zone (buffer depth) explaining 89.36% of deviance. GLM1 containing mean depth at points (site depth) and proximity to the 200m isobaths explained 87.79% of deviance of aggregation sites. Gradient at points (site gradient) and proximity to 1,000m which were left in GLM2 after stepwise reduction explained 86.14% of aggregation site deviance. Diagnostic plots were checked for outliers and showed the residuals were close to the line and Cook's Distance values below 0.5 for all points, suggesting no single point had an overpowering or unnecessary influence on the overall trend of aggregation site presence. P[D] values for all models were high, suggesting the minimum adequate models used explain no less deviance than the full GLMs and the stepwise reduction of variables was justified.

Table 3.1. Binomial generalised linear models of aggregation site presence and absence bathymetric and environmental predictor variables. Statistics include the percentage deviance explained (%D), probability of deviation ($p[t]$) and the probability

of decreased deviance explained from the full model (p[D]). Bold variables indicate significance to a level of 0.05.

Model Name	Predictor Variables Tested	Minimum Adequate Model
GLM1	Site Depth, 200m, SST, Chlorophyll, Site Curvature, Bathymetric Complexity	Site Depth: %D = 0.7549, p[t]= 0.0156, 200m: %D = 0.7475, p[t] = 0.0398, (AIC = 21.9, %D = 0.8779 , p[D] = 0.661)
GLM2	Site Gradient, 1000m, SST, Mean Curvature, Depth Range, Max Gradient	Site Gradient: %D = 0.6523, p[t]= 0.0017, 1000m: %D = 0.4704, p[t] = 0.0149, (AIC = 24.1, %D = 0.8614 , p[D] = 0.794)
GLM3	Buffer Depth, Buffer Gradient, 1000m, Convexity, Concavity	Buffer Depth: %D = 0.8936, p[t]= 0.036, (AIC = 14.9, %D = 0.8936 , p[D] = 0.782)
GLM4	Buffer Gradient, Buffer Max Depth, 200m, Chlorophyll	Buffer Max Depth: %D = 0.3852, p[t]= 0.0009, (AIC = 86.029, %D = 0.3852 , p[D] = 0.529)

4 Discussion

4.1 Bathymetry at aggregation sites

During the data exploration three sites were removed from analysis due to appearing as outliers and skewing the dataset. The Gulf of Mexico aggregation which occurs over deep water (~300m) rather than shallow areas. This is due to high productivity from runoff in the Mississippi Delta (Hoffmayer *et al.*, 2007). The aggregation at Christmas island occurs in shallow water, however as the island is volcanic, it steeply rises from deep water with an average gradient of ~30 degrees, which is considerably steeper than all other aggregation sites (Fairbridge, 1955; Hobbs *et al.*,

2009). Finally, the aggregation in the Al-Shaheen oil field, Qatar is in a relatively flat and shallow area of the Persian Gulf around 12km from deeper water (Robinson *et al.*, 2013). These three aggregations illustrate that although the majority of aggregations follow trends in bathymetry, there are exceptions.

With these three sites removed a number of bathymetric aspects have been shown to be significantly different at and around areas *Rhincodon typus* aggregate compared to areas aggregations do not occur. Aggregation sites were significantly shallower over both spatial scales (point data and the 20km buffer zone area).

Despite the area surrounding aggregation sites being roughly 500m shallower than that measured at non-aggregation sites, the mean distance of aggregation sites to both the mesopelagic and bathypelagic zones was significantly closer by two orders of magnitude than non-aggregation sites. The slope gradient at aggregation sites was shallow and increased when the 20km buffer zone was considered. These results suggest three aspects of bathymetry are important to aggregation formation; shallow areas at aggregation sites, proximity to deep water and slope gradient.

4.2 Shallow coastal water

Site depth and buffer zone depth were among the biggest drivers of aggregations. Literature extensively illustrates *R. typus* aggregating in shallow water with two main reasons. Primarily to feed, hence chlorophyll-a concentration being included in this

study as an indicator of planktonic productivity (Platt and Herman, 1983; Armstrong *et al.*, 1995). However non-aggregation sites had a mean chlorophyll-a concentration twice as large as that at aggregation sites. The mean chlorophyll-a concentration at aggregation sites of 0.7 mg/m³ can be considered relatively high compared to pelagic areas, nevertheless it was lower than other coastal areas within *R. typus*' range. One reason for this can be attributed to the diversity of *Rhincodon typus* prey; aggregations occur at a number of sites exclusively to feed on coral spawn such as Ningaloo reef, Australia (Wilson *et al.*, 2001), Lutjanidae spp. spawn in Belize (Heyman *et al.*, 2001) and Scombridae spp. spawn at the Yucatan peninsula (de la Parra Venegas *et al.*, 2011). Fish and coral spawning events occur in reef areas, typically found in shallow coastal water, hence the presence of *R. typus* aggregations.

Another reason suggested for aggregations in shallow waters is for thermoregulation after deep dives into cooler water. Research into this field is limited (Brunnschweiler *et al.*, 2009; Thums *et al.*, 2012), however this is a viable theory, and the results of this study illustrate aggregations occurred in warmer waters than the random non-aggregation sites selected, although SST was only higher by ~0.5°C. A number of ectothermic species require surface intervals to raise body temperature to levels needed to regulate physiological processes after time spent foraging in cooler, deep waters (Thums *et al.*, 2012). The size of *R. typus*' gills make them extremely efficient at filtering prey from the water, but the large volume of water passing over the gills

causes *R. typus* to cool relatively quickly when in deeper water (Colman, 1997; Stevens, 2007). If thermoregulation occurs in warm shallow areas with high productivity, or an abundance of prey, *R. typus* can continue to feed whilst increasing body temperature from deep dives.

4.3 Deep water

The proximity of *Rhincodon typus* aggregations to deep water is thought to be due to frequent deep dives for prey, whilst remaining close to shallow areas of high productivity for thermoregulation as previously discussed. All aggregation sites in this study were significantly closer to areas with water in the mesopelagic and bathypelagic zones. The deep water bathymetric variables (site depth, buffer depth and proximity to the 200m and 1,000m isobaths) explained the greatest deviance of *R. typus* aggregation site presence, showing these aspects are highly important.

A number of studies with tagged whale sharks show their deep diving behaviour; Rowat and Gore, (2007) recorded three *R. typus* individuals spent ~30% of their time at depths of 750–1000m. Reflected in a study by Brunnschweiler *et al.*, (2009) where two whale sharks were tagged and recorded as deep as 1286m in temperatures of 3.4°C and similarly Wilson *et al.*, (2006) tagged 19 individuals that dived to 980m and in temperatures of 4.6°C. Graham *et al.*, (2006) carried out a similar study, further illustrating deep diving behaviour and also recording available prey at these depths. It has been suggested *R. typus* feeds on zooplankton (euphausiids and myctophids),

squid and jellyfish in these deep waters seaward of the shelf breaks (Graham *et al.*, 2006; Wilson *et al.*, 2006).

Similarly, the basking shark (*Cetorhinus maximus*) and megamouth shark (*Megachasma pelagios*) have also been recorded diving into the mesopelagic and bathypelagic zones in search of prey (Nelson *et al.*, 1997; Sims *et al.*, 2003; Gore *et al.*, 2008). Wilson *et al.*, (2006) hypothesise the deep diving behaviour in all three species is to locate the deep scattering layer and associated prey at dusk and dawn. Further supported by Gore *et al.*, (2008) suggesting the regular dives of increasing depths is indicative of systematic foraging, supporting a number of theories that deep dives occur to locate horizontally dispersed prey. However, despite research into deep diving of these shark species, the function of deep dives for *R. typus* remains largely unknown.

4.4 Slope gradient

Aggregations occurred in relatively flat areas with a mean gradient 0.77 degrees, however it was significantly steeper than non-aggregation sites. Gradient increases further from aggregation sites with a mean of 1.6 degrees and maximum of 29.84 in the 20km buffer zone. Aggregations typically occur in the fore reef and lagoon areas, leading out to the reef slope, reef wall or continental slope which has a steeper slope gradient and deeper water.

Areas of increasing gradient are known to induce upwelling events (Zavala-Hidalgo *et al.*, 2006), particularly coastal areas where depth changes rapidly forcing off shore deep water currents to deflect against the steep slopes, bringing nutrient rich water to the surface (Jacox and Edwards, 2011; Connolly, 2013). These areas have biological significance; often associated with enhanced primary productivity, therefore increasing plankton abundance and attracting a number of species throughout the trophic levels.

Wolanski and Hamner, (1988) carried out one of the first studies on the biological impacts of steep bathymetry, suggesting these areas of great significance to large marine species due to availability of prey. Sims, (2008) confirmed this with *Cetorhinus maximus*, as steep gradients were shown to be their most common foraging habitat, where the highest zooplankton densities were observed. McKinney *et al.*, (2012) modelled the feeding habitat of *R. typus* aggregations in the Gulf of Mexico, showing areas close to the continental shelf are often selected as aggregation sites due to their productivity. The subsequent model that McKinney *et al.*, (2012) created suggested proximity to a continental shelf is one of the biggest influencers on aggregation site location.

4.5 Limitations

Despite the clear results of this study, there have been a number of limitations with available data. The bathymetry data used was the highest resolution freely available, however this was a low resolution dataset, with each pixel representing 1km.

Aggregations can often be in areas as small as 1-5km² (Heyman *et al.*, 2001)

therefore to accurately represent the true bathymetry in aggregation areas, a much higher resolution dataset would be needed. Another limitation was the chlorophyll-a data; the satellite sensors cannot penetrate deeper than 60m (Mélin and Hoepffner, 2011), causing deep water areas with high productivity such as around slopes and shelves to be missed. These areas have been shown to be highly important to *R.*

typus and their aggregations, therefore data showing the productivity in these areas would be useful for future research into *R. typus* aggregations and their deep diving behaviour.

4.6 Implications for conservation

Because *R. typus* aggregate in only a few areas and aggregation events are highly predictable, these sites should be focal points for conservation efforts to protect this species. By showing that aggregations occur in areas with very specific bathymetry, there is the possibility to use species distribution models to predict other suitable areas aggregations may already occur or areas aggregations may shift to with projected climate changes.

Aggregations increase vulnerability to capture and overexploitation, particularly during crucial periods in their lives, such as feeding events and breeding. Whilst there is no evidence *R. typus* aggregations are for breeding, there is an extreme lack of information regarding the breeding behaviour of this species. Therefore, it is plausible aggregations could also be used for mating, which has been observed in zebra sharks (*Stegostoma fasciatum*) (Dudgeon *et al.*, 2008) and is suspected to occur at *Cetorhinus maximus* aggregations (Wilson, 2004). This study has shown bathymetry drives *R. typus* aggregations, mirrored by other studies showing significant increases in *Cetorhinus maximus* abundance around certain bathymetric features. Similarly, this is reflected in cetacean studies, showing an increase in humpback whale, Risso's dolphin and white-sided dolphin abundance around similar features (Allen, 1994; Baumgartner *et al.*, 2001; Yen *et al.*, 2004). As Bathymetric features are of great importance to a number of marine megafauna species, more research should be carried out in this field with conservation efforts focusing on areas where species are at their most vulnerable.

5 Conclusion

This study shows clear evidence that there are significant differences in bathymetry between areas *R. typus* aggregate compared to the rest of their global range where aggregations do not occur. This suggests that aggregations occur with a specific set of bathymetric requirements; shallow areas in close proximity to a reef slope or shelf

break with steep gradient, which leads into water in the mesopelagic and bathypelagic zones. The bathymetric features at and around aggregation sites all directly influence productivity and prey availability, which are the reason *R. typus* and a number of other species aggregate. Knowing this, future conservation efforts for marine megafauna should look for bathymetric features which have continuously been shown to drive aggregations of a number of species. The latest addition to that research is this study which has shown bathymetry does drive whale shark aggregations.

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Declaration

I hereby declare that this dissertation is my own original work. I have acknowledged all sources used and have cited these in the reference section.

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