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Age and Growth of Whale Sharks (Rhincodon typus) near the South Ari Atoll, Maldives

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Abstract

The whale shark (*Rhincodon typus*) has a global distribution in warm to warm temperate oceans, and is a species of high conservation concern currently categorized as Endangered on the International Union for Conservation of Nature (IUCN) Red List. Despite its dire conservation status and concerns about the growing number of ecotourism interactions with this species worldwide, relatively little information is available on key aspects of whale shark biology such as growth rates, reproductive rates, survival rates and breeding habitats. In particular, critical information such as age and growth of whale sharks is needed to improve the management and conservation of this species. Robust knowledge of life history parameters is needed to improve demographic models for whale sharks and enable better evaluation of their vulnerability to fishing pressures and recovery from population declines.

Whale sharks are well known to form aggregations in specific locations, with one such site being the South Ari Atoll in the Maldives. My study aimed to expand knowledge of the population dynamics, including age and growth, of whale sharks at the South Ari Atoll by calculating growth parameters and rates from encounters with free-swimming sharks over a decade (April 2006 to May 2016). A total of 1545 encounters with 125 individual sharks were recorded during this time period. To obtain the most accurate information on the sizes of whale sharks, total lengths were estimated by three different measurement methods (visual, laser photogrammetry, and tape), and linear regression was utilized to investigate how these different methods compared to one another. The results showed that visual estimates tended to underestimate sizes of the larger sharks, and laser and tape measurements yielded similar results to one another ($R^2 = 0.824$). New sharks observed at the South Ari Atoll during the study period were significantly smaller than returning sharks, suggesting that young sharks may be recruited to the South Ari Atoll, where they stay and grow until reaching maturity before leaving the area.

To the best of my knowledge, my study is the first to infer growth parameters and rates from measurements of free-swimming whale sharks. Estimates of von Bertalanffy growth parameters for combined sexes, calculated from 180 encounters with 44 individual sharks (Males (n=40), Females (n=4), TL=3.16 m – 8.00 m), yielded an L_∞ of 19.56 and a k value of 0.021. Analyzing 177 encounters with 40 male sharks (TL=3.16 m - 8.00 m) exclusively provided an L_∞ of 18.08 and a k value of 0.023. These values correspond to a male age at maturity of ~25 years and a longevity of ~140 years, exceeding those estimated for whale sharks captured off Taiwan based on analysis of biannual vertebral rings (male maturity =17 years; longevity (combined sexes) = 80.4 years). There have been few growth studies, mainly from vertebral analysis, that have produced wide ranges in L_∞ (14 – 20.5) and k values (0.017 – 0.037). These differences underscore the need for additional regional studies to obtain population specific estimates of these key life history parameters.

Keywords: von Bertalanffy, laser photogrammetry, growth rate, total length

1. Introduction

The whale shark (*Rhincodon typus*) is the largest fish in the world measuring up to 18.8 m in total length and weighing up to 34 tons (McClain *et al.*, 2015). Whale sharks are one of the three large, filter-feeding sharks, and feed primarily on planktonic and small nektonic prey (Norman, 1999). This species has a broad geographic range and can be seen in tropical and temperate seas between latitudes 30° N and 35° S (Norman, 1999). Whale sharks are oceanic and coastal in habitat and are seen both offshore and regularly inshore near coral reefs. They are often encountered close to the surface of warm waters but have been reported to regularly dive to several hundred meters, with a maximum depth of 1928 m (Tyminski *et al.*, 2015; Thums *et al.*, 2012).

Whale sharks exhibit slow growth, late maturation and long lifespans, which make them highly vulnerable to population declines even when experiencing low levels of exploitation (Compagno, 2001). The IUCN *Red List of Threatened Species* lists whale sharks as Endangered, and the species has experienced a population decline of greater than 50% in the past 75 years (Pierce and Norman, 2016). A number of commercial fisheries for whale sharks closed in the late 1990's and early 2000's, however, whale shark products are highly valuable and the species is still harvested in many countries (Pierce and Norman, 2016).

Despite these conservation concerns, there are still substantial gaps in our knowledge about whale sharks due to limited data on their biology and ecology, thus making it difficult to fully understand population health and sizes (Jeffreys *et al.*, 2013). There is a paucity of information on whale shark reproduction, as well as breeding and pupping locations (Holmberg *et al.*, 2009). The majority of coastal whale shark aggregations are comprised of immature males and there is a lack of information as to where female whale sharks are located. This distributional bias at the known aggregation sites may have implications of habitat selection between the sexes. Whale shark migration is also poorly understood and there have been no major linkages demonstrated between whale shark aggregation sites. Age at maturity, gestation period and number of pups produced in a female's lifetime are poorly understood life history aspects.

Determining life history parameters is vital for improving whale shark management and conservation (Rohner *et al.*, 2015). Knowledge of the age and growth of a species allows for better understanding of age at maturity, lifespan and mortality. These parameters are crucial in determining population sizes and status of the species. It is also important to note that while genetic evidence thus far supports a single genetic population of whale sharks in the Indian Ocean, there have been no confirmed movements of animals between the Eastern and Western Indian Ocean (Rohner *et al.*, 2015). Better understanding of age and size distributions of whale sharks throughout the Indian Ocean will make a key contribution to understanding their ecology and movements**.**

For whale sharks, there have only been a few age and growth parameters derived from studies of vertebral rings. Hsu *et al.* (2014) analyzed vertebrae from the Northwest Pacific and found an L_∞ of 16.8 and a k value of 0.037. Wintner (2000) analyzed vertebrae from stranded whale sharks in South Africa and determined two different von Bertalanffy growth models. The two curves had an L_∞ of 19.66 and 14.96 and a k value of 0.021 and 0.032, respectively. Pauly (1997) reported a tentative L_∞ of 14 and a k value of 0.030. Determining age and growth from vertebral ring counts, however, suffers from the major drawback of needing to obtain vertebrae from dead sharks.

Preliminary research into growth rates of free-swimming whale sharks in the Maldives from 2006 through 2008 has suggested a growth rate of 0.45 m/yr (n=13, Riley *et al.*, 2010). This rate is relatively similar to growth rates estimated from the analysis of vertebrae from whale sharks in the Northwest Pacific, which were reported as 0.60 m/yr after birth that slowly declined to 0.29 m/yr by age twenty (Hsu *et al.*, 2014). Furthermore, Pauly (1997) suggested a growth rate of 0.398 m/yr after birth that declined to 0.225 m/yr by age 20. However, there have not been accurate values of age and growth determined from free-swimming whale sharks with most age and growth data coming from observation in aquaria or vertebral analysis. The comparison of growth rates between locations is important to understand the population dynamics of this species.

One way to learn more about whale sharks is to focus on areas where they form aggregations. Many of these aggregations are seasonal and occur in different locations around the world in response to local increases in food availability linked to spawning events of prey species (Heyman *et al.*, 2001). Some of these aggregations, which often have no more than a few hundred whale sharks, are being extensively studied to gain insights into important life history parameters (Compagno, 2001).

Knowing the location of aggregations is important, but it is also necessary to be able to identify individual whale sharks to track their movement dynamics. Whale sharks have unique pigmentation comprised of many lines and spots. This natural patterning does not change throughout their lifetime, and has proven useful for photo identification of individuals (Norman, 1999), including tracking each whale shark over wide geographic areas and time spans (Arzoumanian *et al.*, 2005). Population dynamics and growth rates can also be studied via the repeated identification of individual whale sharks over time.

My study focuses on whale sharks that aggregate at the South Ari Atoll, Maldives. Whale sharks occur year-round at this site, where the Whale Shark Research Programme (MWSRP) has been collecting data on this aggregation for over ten years (Cagua *et al.,* 2014). Reliable identification of individual whale sharks coupled with encounter data spanning ten years can help provide insight into age and growth of free-swimming whale sharks as there are many re-sightings of the same individuals. The reason(s) why whale sharks are seen in the Maldives year-round while other aggregation sites are seasonal is unknown. In order to further understand the reason(s) why whale sharks aggregate in the Maldives, a better grasp of the age and sizes of the sharks encountered is needed. Investigating the average sizes of new, transient and returning sharks will allow an improved understanding of the sizes and ages of sharks that stay or just pass through. It is hypothesized that small whale sharks may be recruited to the South Ari Atoll and stay in the Maldives until they reach maturity, at which point they leave the area (Pers. comm. R. Rees). Preliminary research done in the Maldives in 2009 suggests that some whale sharks show site fidelity at the South Ari Atoll and that a number of sharks seen here may be year-round or permanent residents of the Maldives archipelago (Riley *et al.*, 2010). However, additional data is needed to confirm this hypothesis.

When determining whale shark sizes and growth rates, it is important to obtain precise and accurate data (Jeffreys *et al.*, 2013). Three different methods are generally used to estimate the total length of free-swimming whale sharks: visual estimates, laser photogrammetry and tape measurements. Some logistical challenges present themselves in the methods used to estimate total length of free-swimming whale sharks, and a comparison of the three methods typically used is important for assessing the accuracy of each method.

Visual estimates are the easiest and most convenient of the three methods to utilize while in the field. However, if visual estimates are not accurate it creates problems with data, analysis, and biological inference. Comparing visual estimates against ostensibly more accurate methods of tape and laser, provide analysis into how reliable visual estimates are to determine total shark length. Human spatial perception is biased underwater and encounters with whale sharks can be short. Therefore, visual total length estimates will likely include significant error even when made by experienced researchers, with the minimum standard error estimated at 0.5 m (Rohner *et al.*, 2011: Jeffreys *et al.*, 2012: Sequeira *et al.*, 2016).

Laser photogrammetry is a non-invasive technique that uses photography to measure objects or animal morphometrics (Deakos 2010). Laser photogrammetry is expected to improve accuracy of whale shark size estimates, with greatly reduced error compared to visual estimates (Rohner et al., 2015). The equipment to carry out laser photogrammetry is simple and allows a single researcher to collect a large number of measurements on a single target. Laser photogrammetry is based on the principle that a laser will project light equidistant apart from the origin. Laser photogrammetry uses two parallel lasers mounted with a camera in the center to project two points of light onto a target that shows a scale of known length to infer the size of the target. However, a drawback of this method is that non-parallel alignment of the laser pointers will cause the scale to change between the laser points depending on the distance from the target. Laser pointers not mounted correctly or that become misaligned during use will create inaccurate measurements leading to incorrect size estimates. Parallax error can be another significant source of error while using laser photogrammetry. It occurs when the laser pointers are not perpendicular to the intended target being measured. Parallax error would lead to an underestimation of whale shark total length. Photographs taken at an angle of 10, 20, 30, 40 and 50 degrees would have corresponding errors of 2.9%, 8.3%, 16.6%, 27.5%, and 39.1%, respectively (Rohner *et al.*, 2015).

Tape measurement is a method often used when sharks are within freediving range of the researchers. However, tape measurements involve collecting data on a free-swimming whale shark, where the shark and the two researchers are all constantly moving. The ability to swim with the shark while ensuring that the two researchers are on the same plane as the shark is not always feasible. If the researchers are not on the same plane as the shark, for example one researcher higher or lower than the other, it can create errors in the measurement. Repeated measurements during an encounter help to reduce these errors. Appropriate diver positioning can be confirmed from photographs taken during encounters. A slack tape measure will also produce an overestimate error while recording the total length of a whale shark. The second researcher positioned at the caudal fin of the shark has to ensure that the slack is removed from the line before the measurement is recorded.

Understanding the relative differences in total length derived by each of the three methods is important for their use in subsequent data analysis and interpretation of data sets from different regions or years. The standardization of data into one measurement approach will allow for the investigation of size trends and growth rates of whale sharks measured utilizing different methods.

2. Objectives

The objectives of my study were to: (1) assess relative accuracy of the three different methods of shark length measurement; (2) determine size differences between new, transient and returning sharks at South Ari Atoll, Maldives; (3) determine the growth rates of the whale shark population at South Ari Atoll and compare them to published growth rates in the literature for other regions.

3. Methods

3.1 Study Area

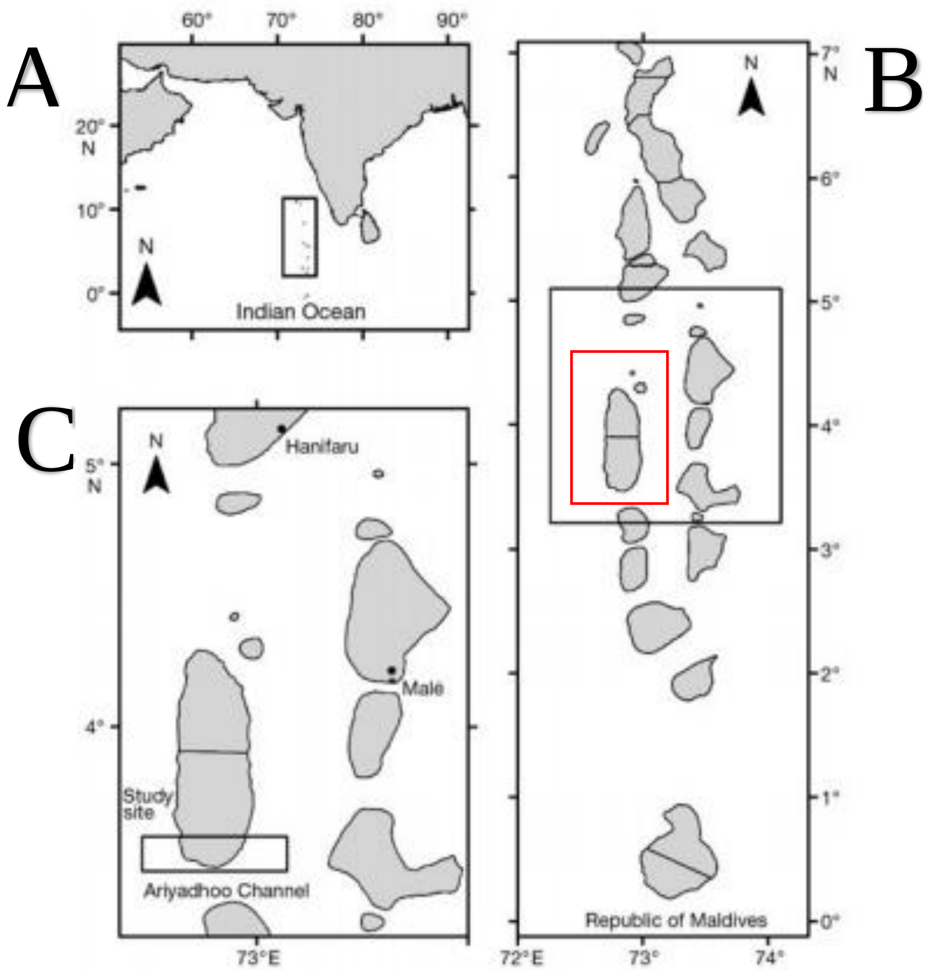

Figure 1: South Ari Atoll, Maldives (figure modified from Riley *et al*., 2010). The Maldives (A), the Ari Atoll (red box in B) and specifically the South Ari Atoll (C) indicates the location of my study.

The study area was located in the South Ari Atoll in the Republic of the Maldives (Figure 1). The South Ari Marine Protected Area (SAMPA), designated in 2009, is the largest MPA in the Maldives with a total area of 42 km^2 (Cagua *et al.*, 2014). The SAMPA extends along the seaward fringe of the South Ari Atoll from Rangali Island to Dhigurah Island. South Ari Atoll, and specifically the MPA, is known for the occurrence of whale sharks throughout the year (Cagua *et al.*, 2014). Surveys for whale sharks were made along the SAMPA from April 2006 to May 2016.

3.2 Study Population

This study site is a unique whale shark aggregation site because animals are encountered year-round, whereas other known aggregation sites in the Indian Ocean are seasonal in nature (Cagua *et al.*, 2014, Rowat, 2007). The MWSRP has been studying whale sharks in the South Ari Atoll, Maldives since 2006 and has accumulated an extensive dataset on this aggregation's size dynamics. To date 295 individual sharks have been identified with numerous re-sightings of the same individuals.

3.3 Surveys

My study followed the protocol described by Riley *et al.* (2010) to locate whale sharks along the SAMPA. When a shark was spotted, researchers were dropped by boat in front of the animal to take photographs, measurements and observe its behavior (Riley *et al.*, 2010). An example of the MWSRP survey sheet and the types of data collected during each encounter is provided in Appendix A. Total length was measured utilizing all three methods whenever feasible. Identification photographs were taken during the encounters and were later analyzed.

3.3.1 Visual Estimates

Total length visual estimates to the nearest 0.5 m were made by experienced researchers at every whale shark encounter. Two or more researchers recorded their estimates and the average was documented in the dataset.

3.3.2 Laser Photogrammetry

Laser measurements were made by utilizing a rig with two lasers set 50 cm apart with a camera mounted in the center. Two green underwater Apinex (BALP-LG05-B150) laser pointers and an Olympus Tough TG 4 camera comprised the laser rig. The lasers projected two points that were visible on the shark when identification photographs were taken. Rohner *et al.* (2011) derived a formula to calculate total length of whale sharks from laser photogrammetry. Total lengths were, therefore, calculated as:

$$\text{Total Length} = \frac{4.8373 \times \text{Length from } 5^{th} \text{ gill to start of first dorsal}}{\text{Pixels per 50 cm} / 50} + 80.994$$

from Rohner *et al.* (2011) and recorded in the temporal dataset. All images that were not perpendicular to the whale shark were excluded from analysis since there is no way to correct for parallax error in the field.

Figure 2: Laser photogrammetry used to determine total length.

3.3.3 Tape Measurements

Tape measurements were made whenever feasible during an encounter. This method involved two researchers diving above the shark to measure the dorsal side, from the tip of the mouth to the end of the caudal fin. One researcher swam with the tape and kept it in line with the tip of the mouth. The other researcher swam towards the caudal fin and removed the slack in the line. The first researcher gave one sharp pull to indicate that he/she was in position while the second researcher gave two sharp pulls to indicate the measurement was taken. This method was done multiple times during an encounter and the average was recorded in order to reduce any associated errors.

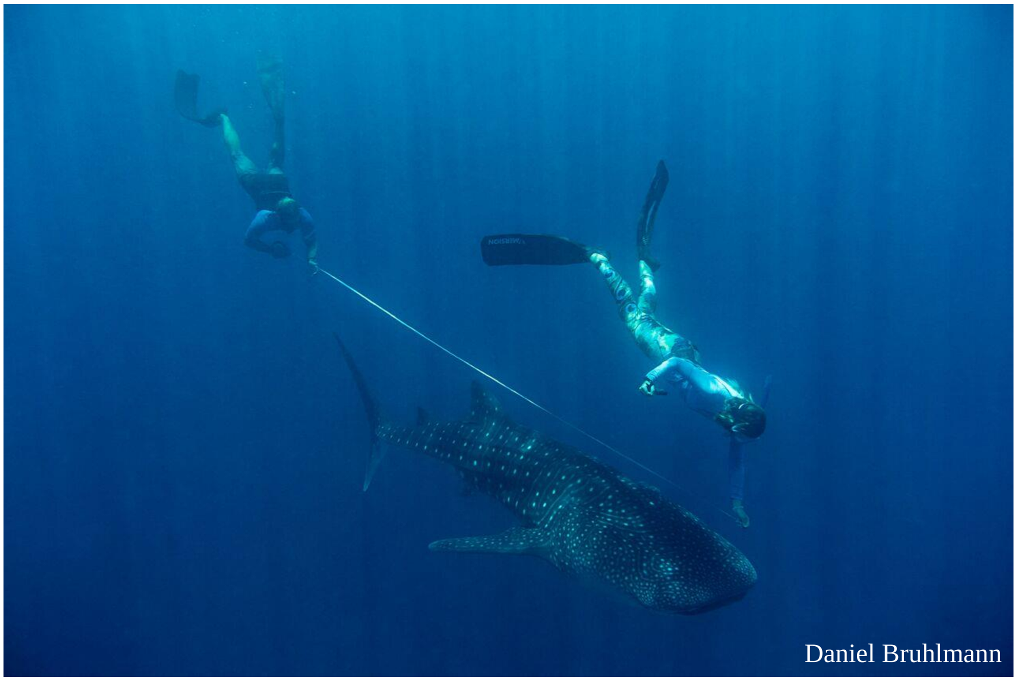

Figure 3: Tape measurement method used to determine total length.

3.3.4 Photo Identification

Photo identification was done on land after the day's survey was concluded. Lateral photographs were taken of each shark with the focal area defined by four distinct boundaries. The boundaries were (1) posterior to the 5th gill; (2) dorsal to the proximal end of the pectoral fin; (3) anterior of a line drawn dorso-ventrally from the posterior end of the pectoral fin to the 3rd longitudinal ridge; (4) ventral of the 3rd longitudinal ridge (Arzoumanian *et al.*, 2005, Riley *et al.*, 2010). A pattern recognition software (I^{3}S, Interactive Individual Identification System http://reijins.com/i3s) described in Brooks *et al.* (2010) was used to find matches between the photographs and whale sharks in the MWSRP database. First, reference points were selected in I^{3}S. Reference point one was the top of the 5th gill, point two was where the pectoral fin intersects with the body and point three was the bottom of the 5th gill. Once these reference points were defined, then a minimum of 12 white spots were selected to identify the shark. The photograph was then run through an algorithm that provided the closest match from known sharks in the database. I^{3}S showed the top matches from the database to the shark being identified. Successful matches were visually confirmed to prevent any errors.

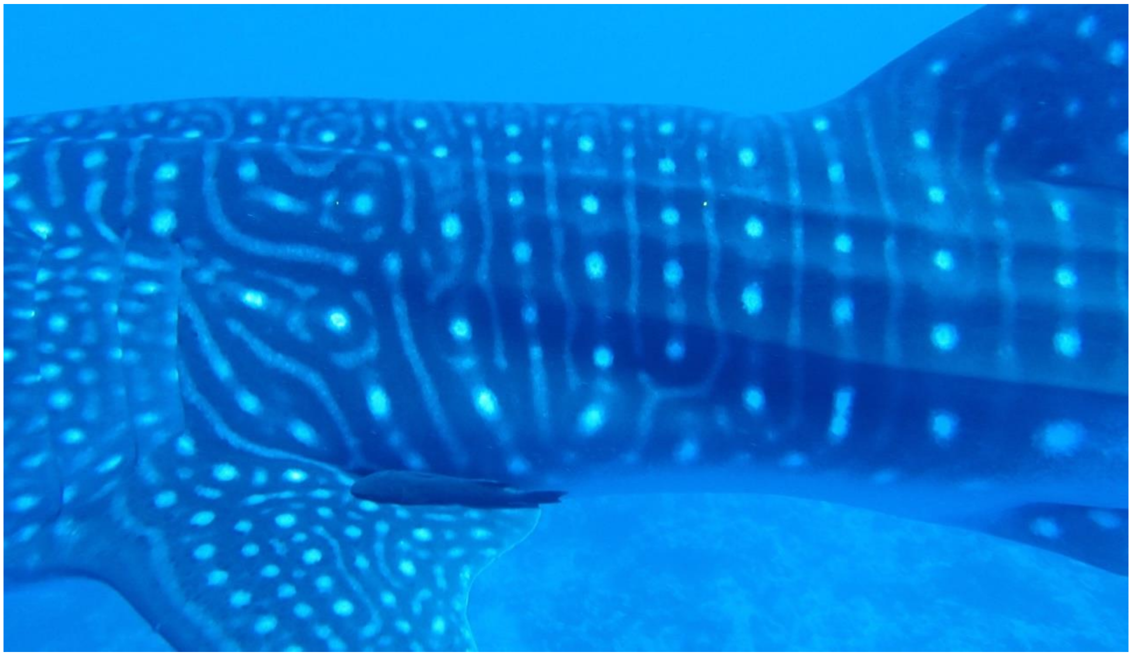

Figure 4: Identification photograph.

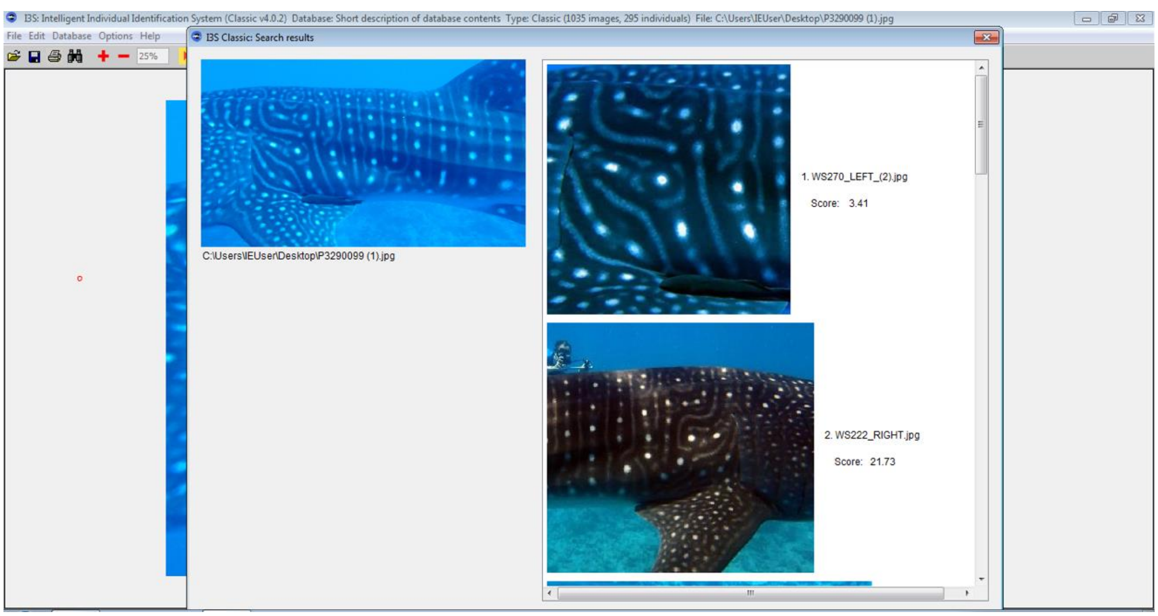

Figure 5: Match of identification photograph and the corresponding photographs in the MWSRP database.

3.3.5 Sex Determination

Sex of the whale shark was determined by recording the absence or presence of claspers. Males have two external reproductive organs called claspers. Females lack these external claspers. Researchers swam down below the caudal fin and determined the sex of the shark.

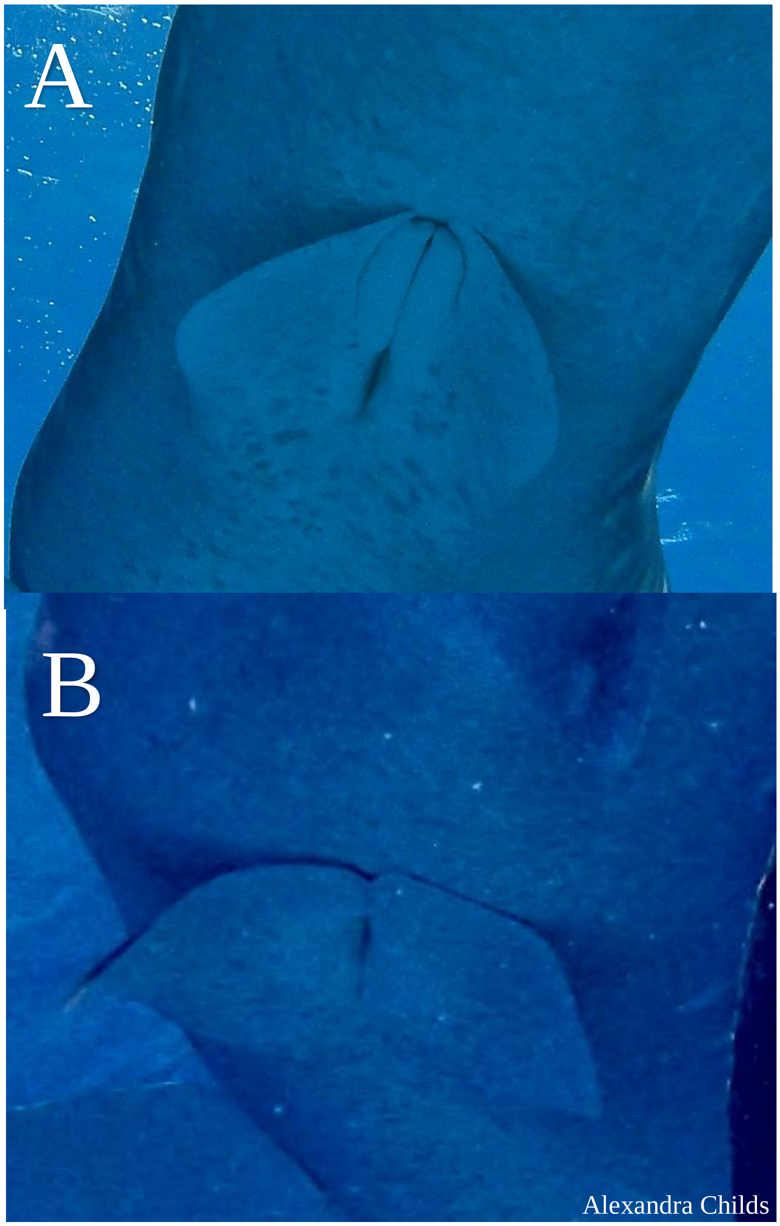

Figure 6: Sex determination. Males are identified by the presence of two external organs, called claspers (A). Females are identified by the absence of these organs (B).

3.4 Statistical Analyses

3.4.1 Regression Analysis

All statistical analyses were performed using R Studio. Encounters that contained documentation of total length with more than one method were used for analyses. The measurement methods were then compared by regression analyses which plotted estimates derived from each method against the other methods to determine the bias on total length estimates.

3.4.2 Precision of tape and laser measurements

The precision of tape and laser measurements was calculated in order to determine the standard error associated with each method. Variance was calculated by subtracting the recorded measurement from the mean of the measurements. Square root of variance was then calculated to provide standard deviations for each.

3.4.3 Differences between New, Transient and Returning Sharks

In the early years of data collection each shark encountered was theoretically a new shark and would therefore skew proper labeling of each shark into new, transient and returning occurrence categories. Therefore, to avoid mislabeling, sharks were only labeled into these categories after the number of new sharks seen per search effort remained constant. There were a total of 16 sharks seen in 2006, the first year of study, and these served as a baseline for analysis of subsequent year observations. In order to be labeled as new or returning, sharks had to be at liberty for at least a year. They were then labeled as new at the first encounter, and as returning for every subsequent encounter. Sharks that were only seen once within a year were labeled as transient (Fox *et al.*, 2013). After the results obtained from comparison of the accuracy of the three measurement methods (see Results for explanation), all shark total length estimates were converted to an adjusted tape measurement. A histogram was plotted and an Analysis of Variance (ANOVA) conducted to compare the average sizes of sharks by category label per year.

A Tukey Post Hoc test was run to determine what would influence the differences in sizes.

3.4.4 Growth parameter determination

Only tape and laser measurements were used to analyze growth parameters. Sharks that were known to have amputated caudal fins were excluded from growth parameter analysis as they would have provided altered growth rates. Laser measurements were converted to tape measurements due to lower variance and error of converting to a different measurement method (see Results for explanation). This was done to standardize the dataset. Tape and laser measurements recorded within the same month were averaged together to further reduce error associated with the measurements. Growth parameters were only calculated for sharks at liberty for at least a year because any small change in size accompanied by a small change in time would yield unrealistic growth rates. Since the age of the animals was unknown, the following nonlinear least squares equation was used to estimate the von Bertalanffy growth parameters:

$$\Delta L = (L_\infty - L_i) * (1 - e^{(-k\Delta t)})$$

where ΔL is the change in size (m), L_∞ is the maximum size (m), L_i is the capture size (m), k is the growth coefficient (yr^{-1}) and Δt is the change in time (yrs) (Quinn and Deriso, 1999; Hart and Chute, 2009). Combined sexes and male only growth parameters were determined.

3.4.5 Age and Growth

A nonlinear regression analysis was used to determine a growth model of whale sharks in the Maldives. These growth parameters were then utilized to produce a two parameter von Bertalanffy growth model. The two-parameter von Bertalanffy growth model is defined by the following equation:

$$L_t = L_\infty - (L_\infty - L_0)e^{(-kt)}$$

where L_t is the total length (m), L_∞ is the maximum size (m), L_0 is the size at birth (m), k is the growth coefficient (yr^{-1}) and t is age (years).

The von Bertalanffy growth model is widely used in the study of age and growth in a variety of fish species, but insufficient sample size of small and large individuals can often cause poor estimates of parameters using this model (Tanaka et al., 1990). Often researchers replace t_0 with L_0 as a stronger two parameter model. Fabens (1965) was the first to introduce this alternate equation and it has provided more realistic estimates where sample size was small (Goosen and Smale, 1997) and has recorded similar parameters to the von Bertalanffy growth model when sample sizes were large (Carlson *et al.*, 2003; Goldman *et al.*, 2012). Similarly, Hsu *et al.* (2014) found that the two parameter von Bertalanffy growth model had a higher Akaike information criterion (AICc) value when compared with other models and provided the best fit for sex-combined data.

There is a wide range of total lengths at birth (L_0) in the literature. Aca and Schmidt (2011) described a 0.46 m fully viable newborn whale shark. A 0.94 m specimen was found in India with an external yolk sac attached, indicating that it was not at full term (Manojkumar, 2003). My study used an intermediate L_0 of 0.64 as this was the largest full term embryo from Joung *et al.* (1996). These authors divided whale shark embryos into three size classes, the largest (0.54 -0.64 m) were free of their egg cases, had their yolk sacs absorbed and appeared ready to be born (Stevens, 2007). Growth rates, age at maturity and longevity were then calculated from the two parameter von Bertalanffy growth model produced from the growth parameters derived from my study.

3.5 Justification of the model

All encounter data were used to determine how the model fit for sharks in the Maldives. Each measurement was converted to an adjusted tape measure total length, as this proved the best fit for both tape and laser measurements (see Results). Once every encounter had an adjusted size, each shark was given an initial age utilizing the two parameter von Bertalanffy equation determined in my study. After the initial age was established from the growth model, each shark was given a new age and new size at each subsequent encounter. All age and length data was plotted with the two parameter von Bertalanffy growth equation determined from my study.

3.6 Longevity

A theoretical method to calculate longevity derived from Taylor (1958) is defined as the age in which 95% of L_∞ is reached. This can be calculated by solving the von Bertalanffy growth equation for t and replacing L_t with $0.95L_\infty$, yielding the following equation:

$$\text{Longevity} = (1/k)\ln((L_\infty - L_0)/(L_\infty(1 - (L_t/L_\infty)))$$

where k is the growth parameter, L_∞ is the maximum size (m), L_0 is birth size (m) and L_t/L_∞ is equal to 0.95 (Hsu *et al*., 2014).

3.7 Age at Maturity

Norman and Stevens (2007) assessed size at maturity of male sharks in Ningaloo, Australia. They found that the length at 50% maturity was 8.1 m while the length at 95% maturity was 9.1 m. Similarly, Colman (1997) found that size at maturity for males was 9 m. Maturity for 50% of male sharks in Mozambique was found to be 9.16 m (Rohner *et al.*, 2015). Beckely *et al.* (1997) analyzed stranded whale sharks in South Africa and found that the largest female at 8.7 m was immature which may suggest that female sharks mature at a larger size than males. The corresponding ages of 8.1 m and 9.1 m from the two parameter von Bertalanffy growth equation derived in my study were used to determine age at maturity.

4. Results

4.1 Regression Analysis

4.1.1 Visual and Laser Measurements Regression

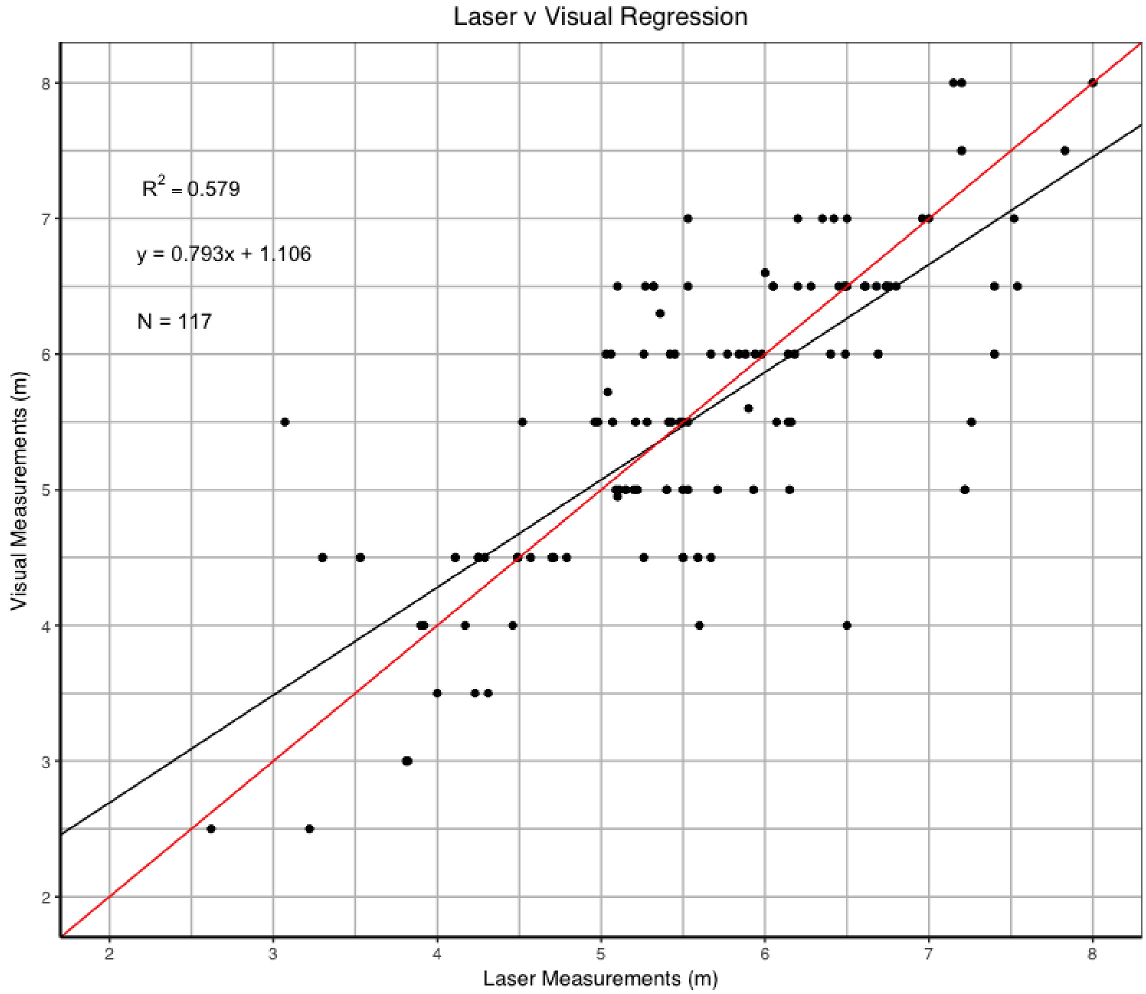

Figure 7: Relationship between visual and laser measurement methods. A red line with a slope of one (perfect match) added for reference.

There were a total of 117 encounters where visual and laser estimates were both recorded. The results showed that visual estimates tended to overestimate the total lengths of 2 m to 5.4 m sharks and underestimated the sizes of 5.4 m to 8 m sharks. The mean of visual estimates was 5.55 m and the mean of laser estimates was 5.60 m. A regression line was produced with the following equation:

Visual Measurements = 0.793*(Laser Measurements) + 1.106 (R^2 =0.579).

4.1.2 Tape and Visual Measurements Regression

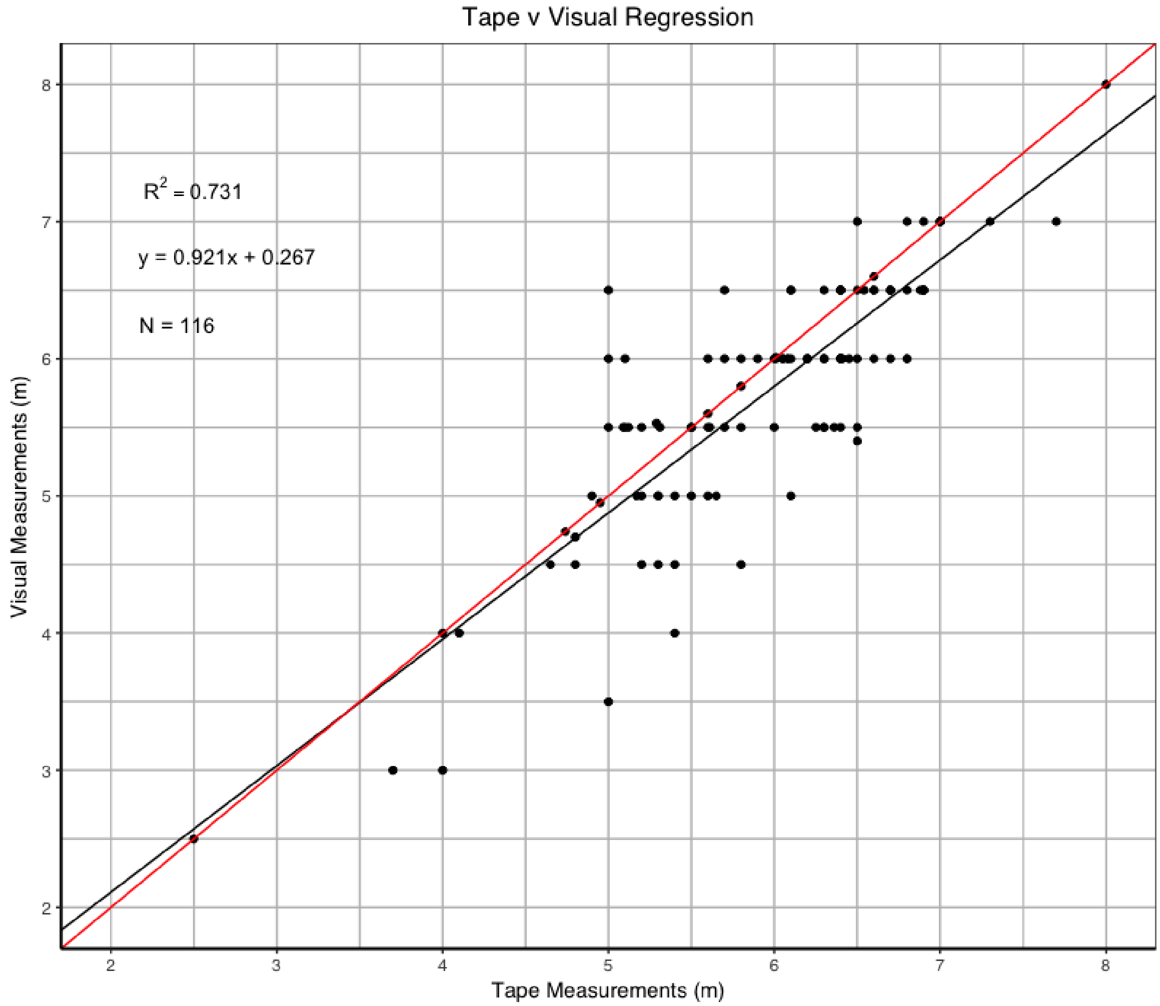

Figure 8: Relationship between tape and visual measurement methods. A red line with a slope of one (perfect match) added for reference.

There were a total of 116 encounters where tape and visual estimates were both recorded. The results showed that visual estimates were good at predicting the total length of sharks between the sizes of 2 m to 4 m. However, visual estimates tended to slightly overestimate the size of sharks larger than 4 m. The mean of visual estimates was 5.75 m and the mean of tape estimates was 5.96 m. A regression line formula was produced with following equation:

Visual Measurements = 0.921*(Tape Measurements) + 0.267 (R^2 = 0.731).

4.1.3 *Tape and Laser Measurements Regression*

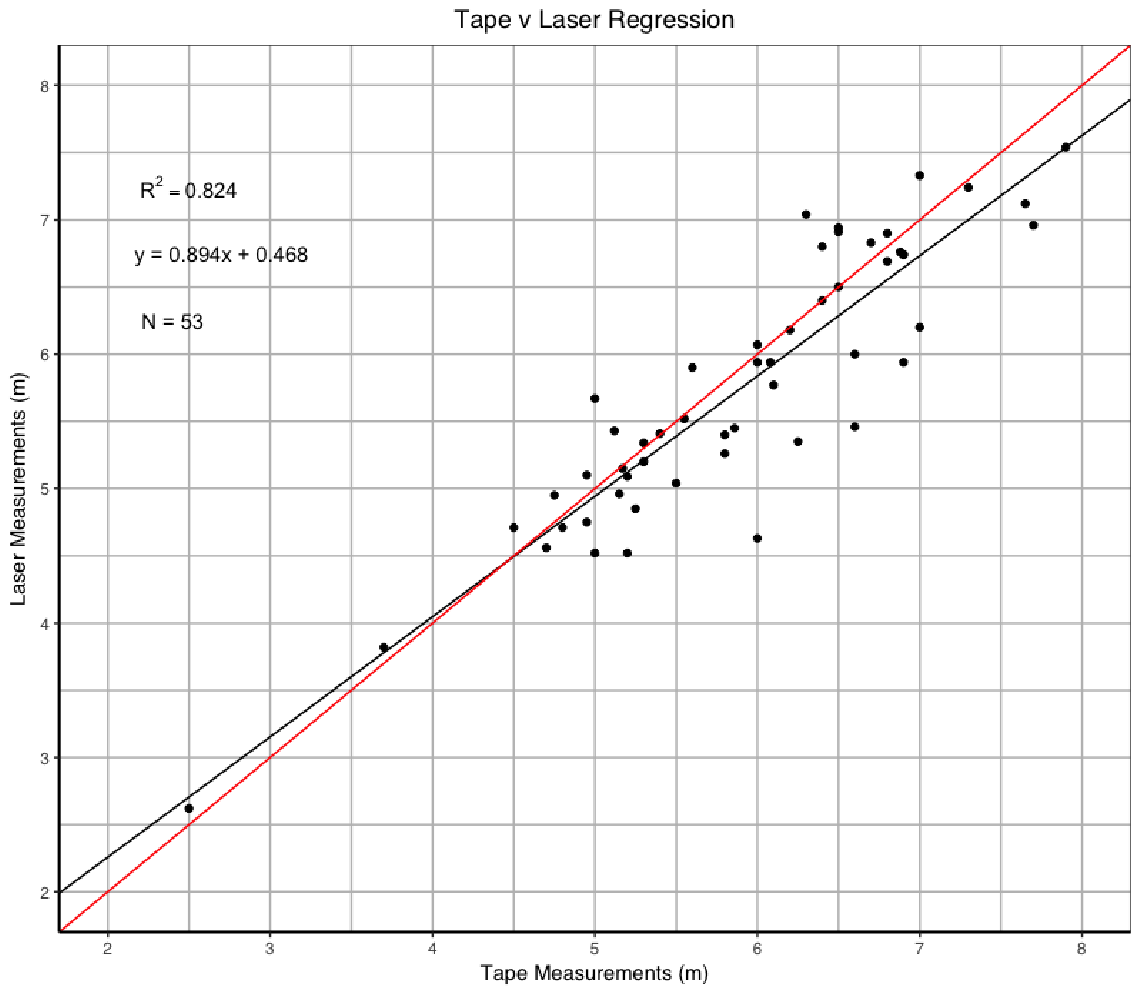

Figure 9: Relationship between laser and tape measurement methods. A red line with a slope of one (perfect match) added for reference.

There were a total of 53 encounters in which tape and laser estimates were recorded. The results showed that laser estimates tended to overestimate the total lengths of sharks from 2 m to 4.5 m in size. They also tended to slightly underestimate sharks larger than 4.5 m. The mean of tape estimates was 5.90 m and the mean of laser estimates was 5.75 m. A regression line was produced with the following equation:

Laser Measurement = 0.894*(Tape Measurement) + 0.468 ($R^2 = 0.824$).

4.2 Precision of Tape and Laser Measurements

Standard deviations were calculated to determine the precision of laser and tape measurements. There were a total of 29 encounters with 98 individual measurements where multiple laser measurements were analyzed. The standard deviation associated with laser measurements was found to be ±0.14 m indicating repeated measurements may differ by this amount. There were a total of 32 encounters where multiple tape measurements were documented. A total of 81 measurements were analyzed and precision was calculated. The standard deviation associated with tape measurements was calculated to be ±0.17 m indicating repeated measurements may differ by this amount.

4.3 Average Sizes of New, Transient and Returning Sharks

A total of 942 survey trips were made between April 21, 2006 through May 8, 2016, which resulted in 1999 encounters with 188 sharks. November 2010 was the point in time where the number of new sharks seen per search effort started to remain constant (Figure 10). July 2013 has a higher encounter rate due to the fact that one day was spent on the water where three new sharks were encountered (Figure 10). It is possible that if there were more days on the water, this high value would have decreased and been more in line with the other encounter rates from November 2010 onward.

There were a total of 1320 encounters with 117 sharks recorded since November 2010. Sixty-nine returning sharks contributed to 1141 of these encounters. Twenty-five transient sharks contributed to 67 of these encounters and 23 new sharks contributed to 23 encounters. There were 89 encounters involving sharks that could not be labeled because a year had not elapsed from their first sighting. An ANOVA was run to investigate the average sizes of sharks by label and year (Table 2). The results show that there was a statistically significant difference in sizes by label. A post hoc test showed that there was only a significant difference between new and returning sharks (Table 3).

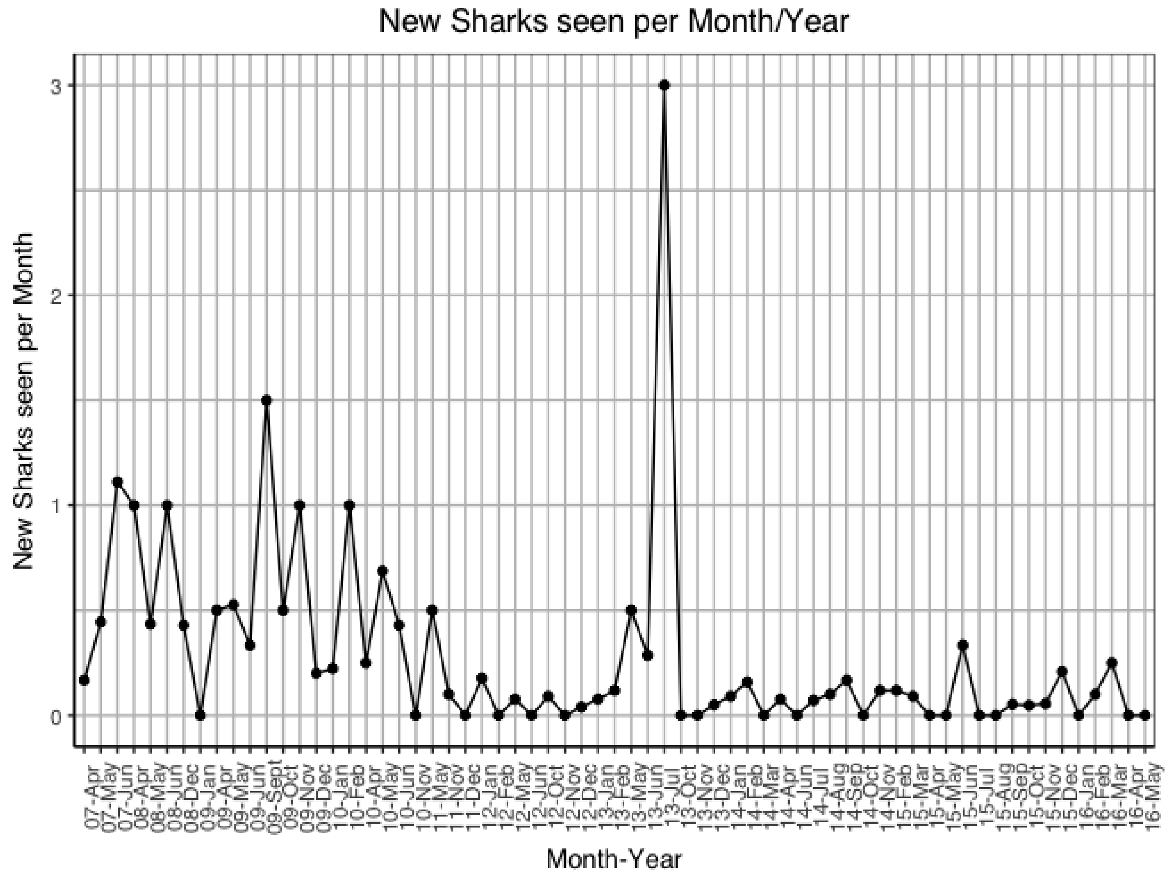

Figure 10: Average number of new sharks seen per search effort (days) throughout each month and year of study.

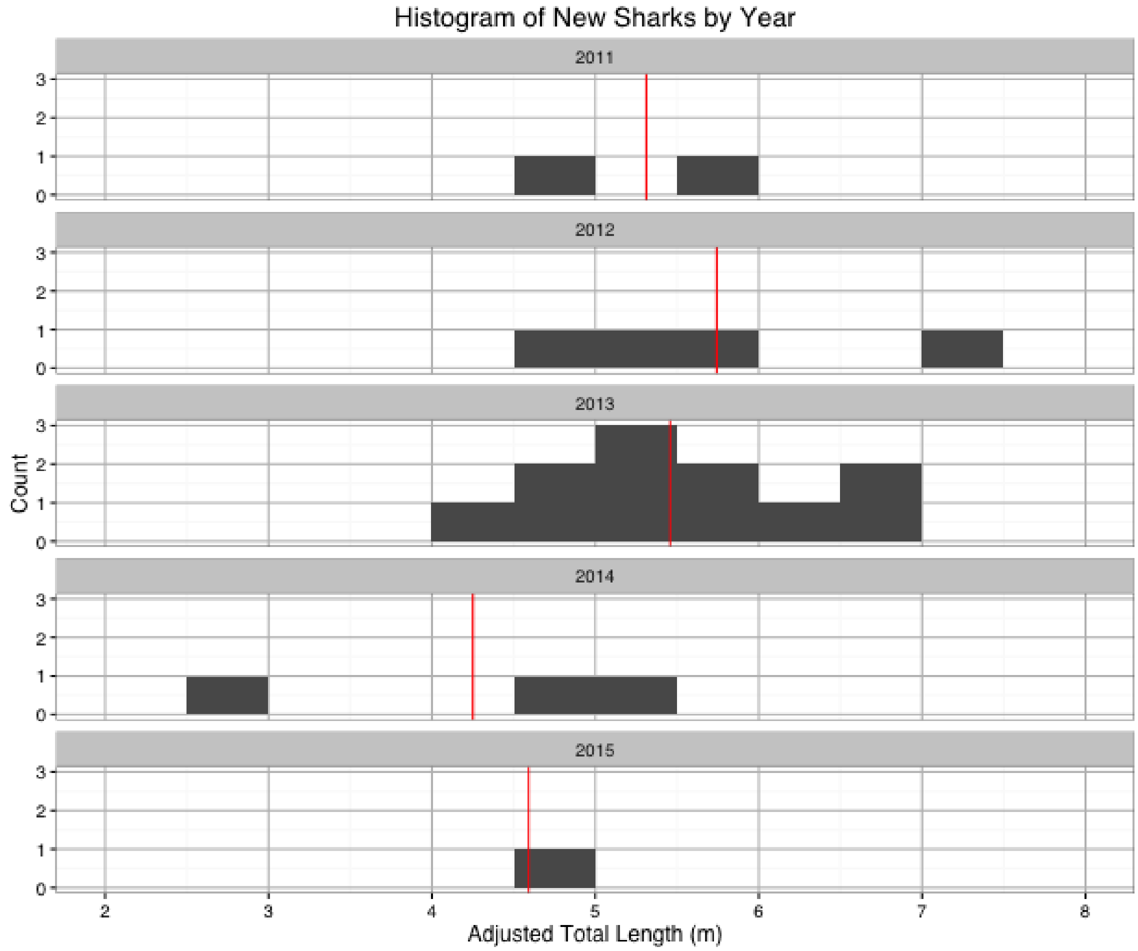

Figure 11: Size frequency of new sharks seen per year. The red line associated with each year is the average size of new sharks seen during that year.

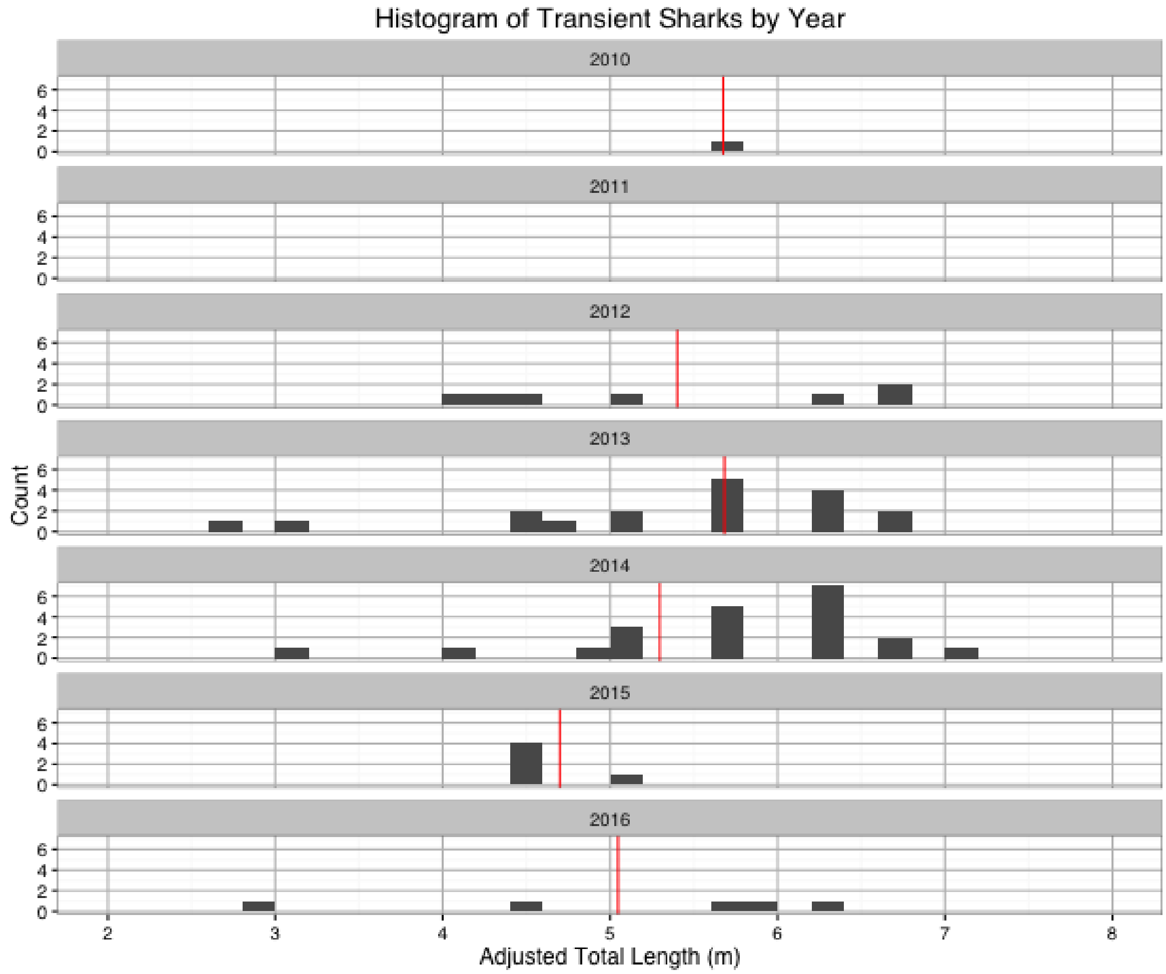

Figure 12: Size frequency of transient sharks seen per year. The red line associated with each year is the average size of transient sharks seen during that year.

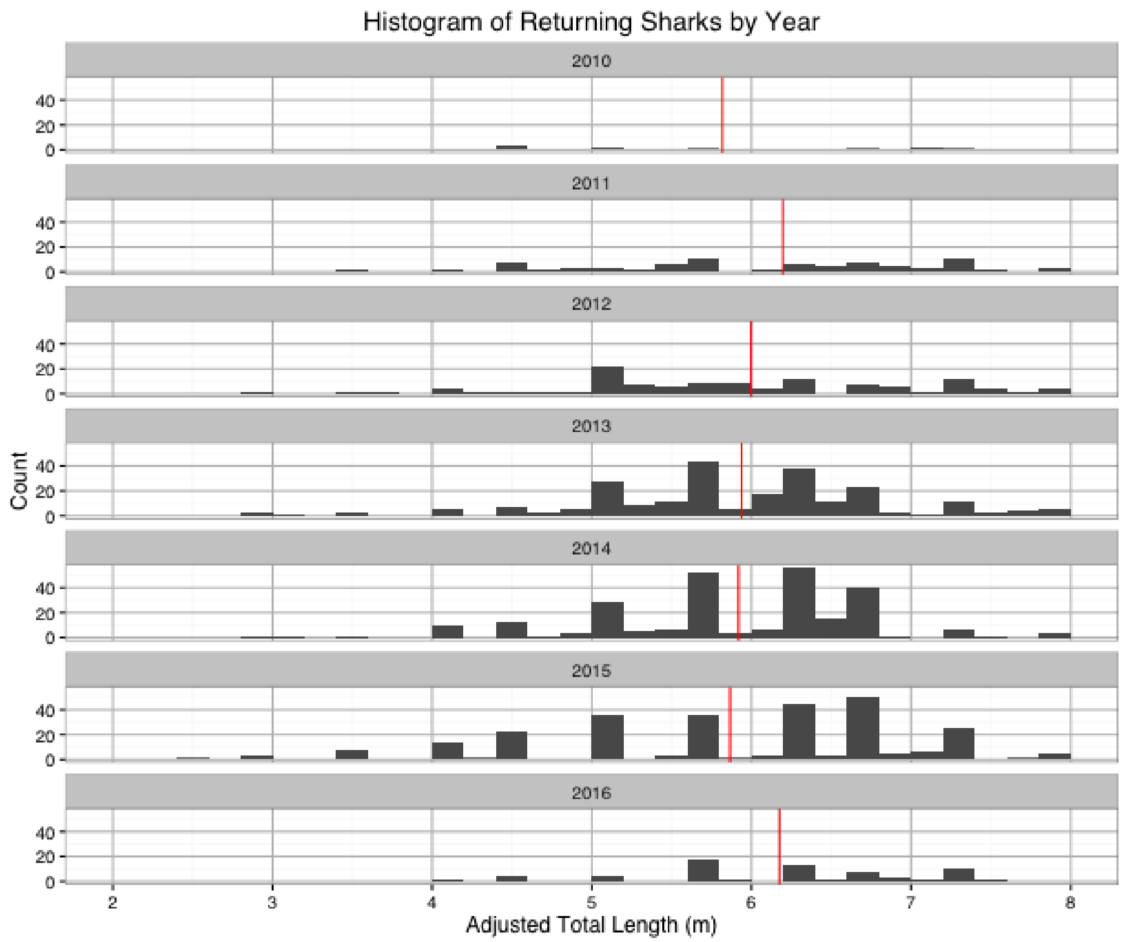

Figure 13: Size frequency of returning sharks seen per year. The red line associated with each year is the average size of returning sharks seen during that year.

Table 1: Summary of average sizes by category label per year.

Year	*New*	*Returning*	*Transient*
2010	--	5.82	--
2011	5.31	6.20	5.68
2012	5.74	6.00	5.40
2013	5.46	5.94	5.68
2014	4.25	5.92	5.30
2015	4.59	5.87	4.70
2016	--	6.18	5.05

Table 2: Results of the ANOVA to investigate label (new, transient and returning) and year.

	DF	*Sum Square*	*Mean Square*	*F Value*	*P*
Year	1	0.0731	0.0731	0.550	0.4794
Label	2	1.9604	0.9802	7.377	**0.0153***
*Year*Label*	2	0.8799	0.4399	3.311	0.0896
Residuals	8	1.0630	0.1329		

* indicates significance level

Table 3: Results from the Tukey Post Hoc test.

	Difference	Lower	Upper	P adjusted
Returning-New	0.8915833	0.14523333	1.63793333	**0.0202881***
Transient-New	0.3992500	-0.4183355	1.2168355	0.4143339
Transient-Returning	-0.49233333	-1.2386833	0.2540167	0.2205241

*indicates significance level

4.4 Growth parameters

A total of 505 encounters with 61 sharks had tape or laser measurements available for analysis. Only four sharks had measurements within one month so growth rates could not be analyzed as there were no subsequent encounters. Averaging the measurements recorded within the same month created a dataset of 308 encounters with 53 sharks. There were 186 encounters with 44 sharks at liberty for at least a year. There were 177 encounters with 40 male sharks and only nine encounters with four female sharks were recorded. Growth parameters were calculated for both sexes combined and then for males separately. Female sharks were not analyzed separately due to the small sample size. Six encounters outside of two standard deviations from the standard residuals were removed from the dataset. Solving the equation gave an L_∞ of 19.56 and a k value of 0.021 for the combined sexes dataset. Only analyzing data from male sharks changed the parameters to an L_∞ of 18.08 and a k value of 0.023.

4.5 Age and Length

An L_0 of 0.64 m total length was applied to the two parameter von Bertalanffy model (Hsu *et al.*, 2014). Adding the values for k and L_∞ derived from the nonlinear equation yielded a two parameter von Bertalanffy growth equation for both sexes of:

$$L_t = 19.556 - 18.916e^{-0.0211t} \qquad \text{(Combined Sexes)}$$

where L_t is total length (m) and t is age (years).

Utilizing the values calculated from only male whale sharks yielded a two parameter von Bertalanffy growth equation of:

$$L_t = 18.081 - 17.441e^{-0.0234t} \qquad \text{(Males)}$$

where L_t is total length (m) and t is age (years).

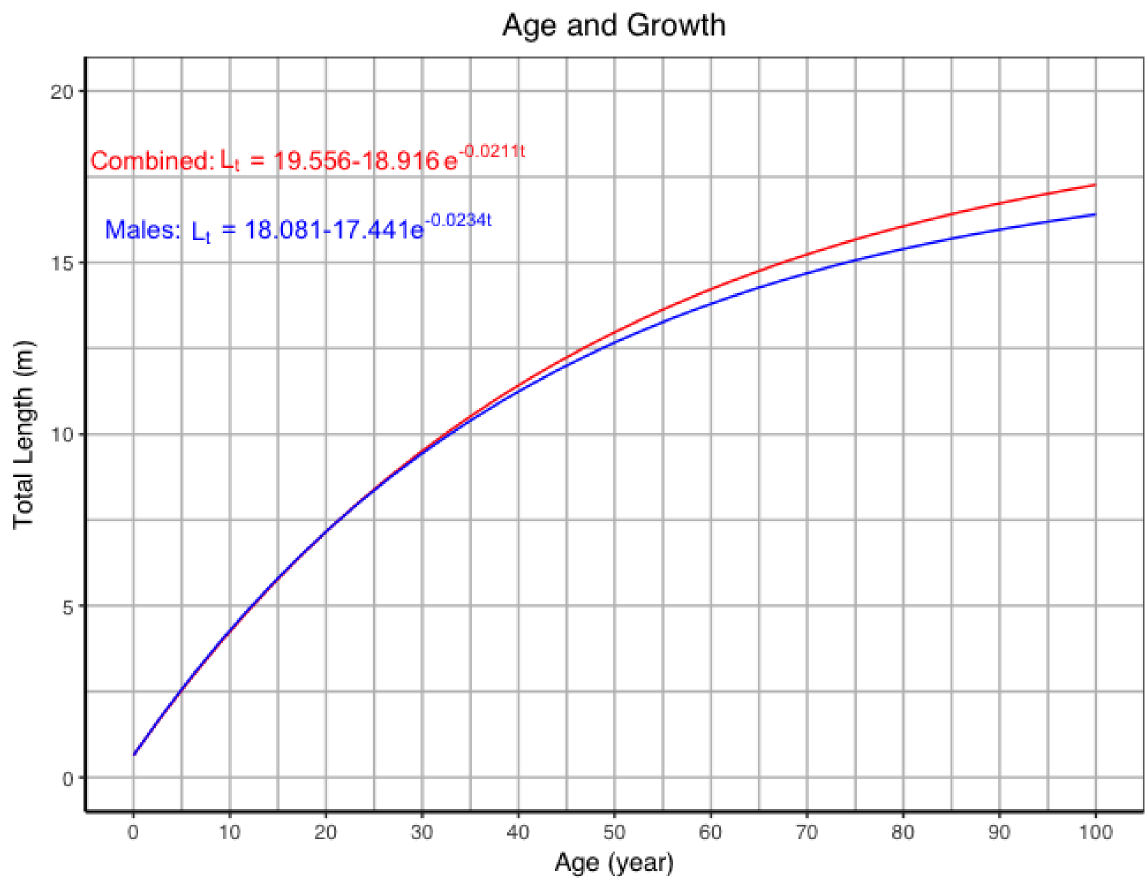

Figure 14: Age and length data from the two parameter von Bertalanffy growth equation utilizing the growth parameters derived from the nonlinear regressions.

4.6 Growth Rates

Growth rates for male sharks during the first year were estimated to be 0.403 m/yr and declined gradually to 0.259 m/yr by age 20 (Table 3). Combined sexes growth rates did not differ much with first year growth estimated to be 0.395 m/yr which declined gradually to 0.265 m/yr by age 20 (Table 3).

Table 4: Age, total lengths and growth rates derived from each two-parameter von Bertalanffy growth equation.

	Males		*Combined Sexes*	
Age (yr)	Total Length (m)	Growth Rate (m/yr)	Total Length (m)	Growth Rate (m/yr)
0	0.640	--	0.640	--
1	1.044	0.403	1.035	0.395
2	1.438	0.394	1.422	0.387
3	1.823	0.385	1.800	0.379
4	2.199	0.376	2.171	0.371
5	2.566	0.367	2.534	0.363
6	2.925	0.359	2.889	0.355
7	3.276	0.351	3.237	0.348
8	3.618	0.342	3.578	0.341
9	3.953	0.335	3.912	0.334
10	4.279	0.327	4.238	0.327
11	4.599	0.319	4.558	0.320
12	4.910	0.312	4.871	0.313
13	5.215	0.305	5.178	0.307
14	5.513	0.298	5.478	0.300
15	5.803	0.291	5.772	0.294
16	6.087	0.284	6.060	0.288
17	6.365	0.277	6.342	0.282
18	6.636	0.271	6.617	0.276
19	6.900	0.265	6.888	0.270
20	7.159	0.259	7.152	0.265

4.7 Justification of Model

All encounters from April 21, 2006 to May 8, 2016 were used to determine whether the model was representative of the actual data. Measurement data was recorded during 1402 encounters with 106 male sharks. The minimum and maximum age determined from the data was 5.5 and 26.4 years, respectively. The mean age of all male sharks encountered was 14.8 years. The minimum and maximum size was 1.88 m and 8.9 m, respectively. The mean size from all encounter data was 5.77 m. Histograms of total length and age were constructed to provide a better understanding of the population demographics of male whale sharks seen at the South Ari Atoll, Maldives (Figure 16 and 17).

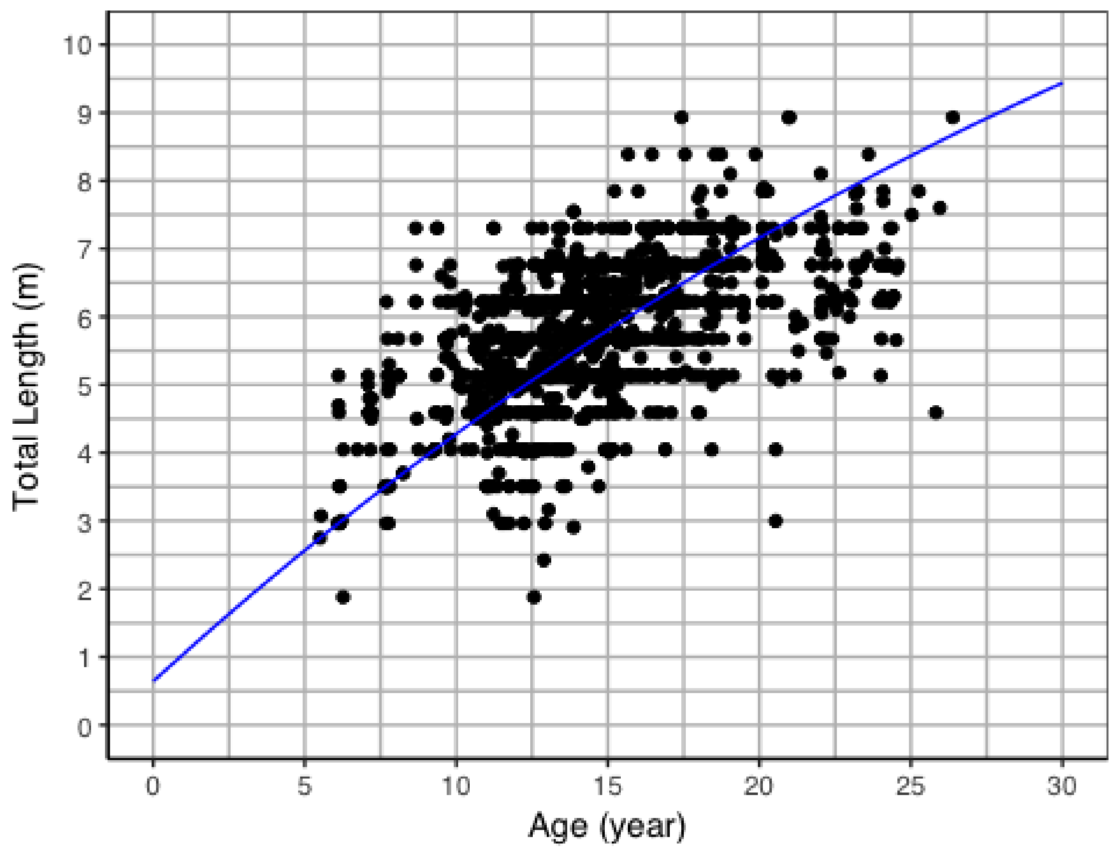

Figure 15: Age and length data for every male whale shark encounter from April 21, 2006 to May 5, 2016. The blue line is the male two parameter von Bertalanffy growth equation determined by the nonlinear model.

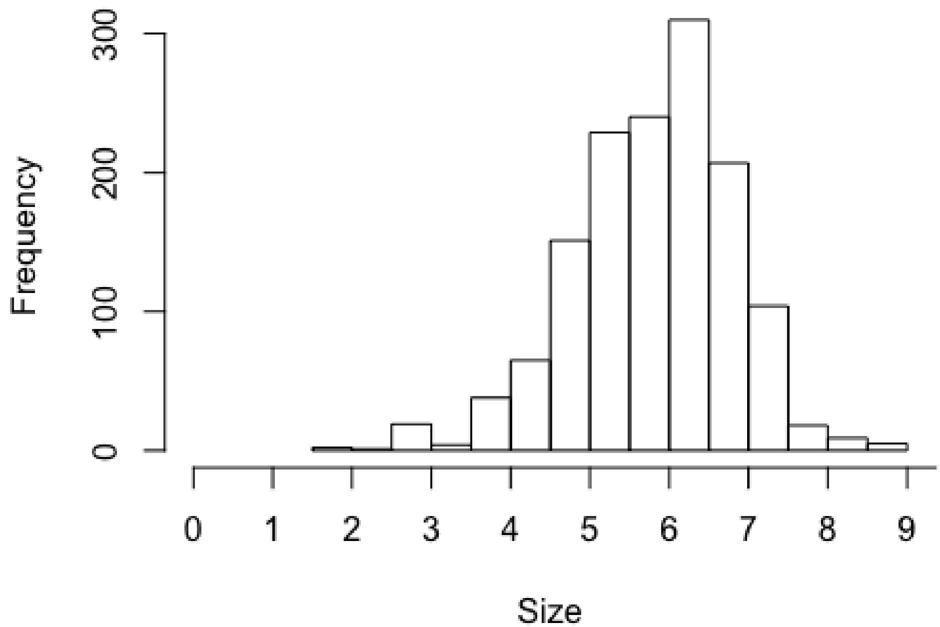

Figure 16: Histogram of total lengths of sharks encountered.

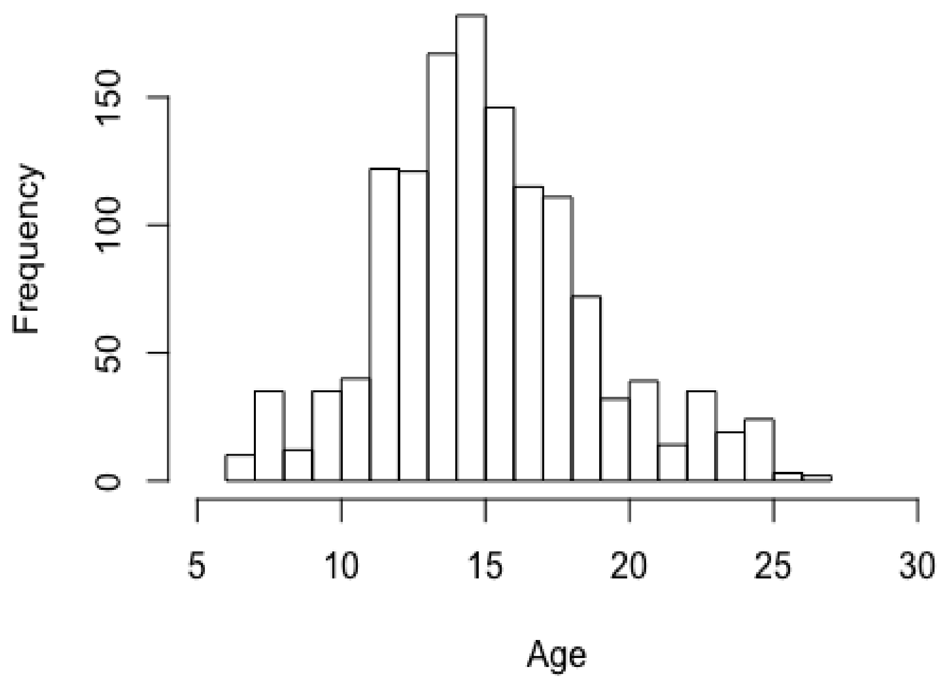

Figure 17: Histogram of ages of sharks encountered.

4.8 Age at Maturity and Longevity

Assuming male whale sharks become mature between 8.1 m and 9.1 m (Eckert and Stewart, 2001), the male growth model estimates the age at maturity to be between 23.85 and 28.36 years, respectively. There were a few sharks in my study that were in this size range, however none were documented as mature individuals based on absence of observed calcified claspers. Use of the Taylor method yielded a longevity of 135.14 years from the L_∞ derived from the male sharks in my study.

5. Discussion

My study analyzed a long-term dataset of length measurements and individual identifications to investigate growth parameters of free-swimming whale sharks in the Maldives. Total length measurements obtained using three different methods were compared and developed into a standardized length unit. This standardization allowed the average sizes of new, transient and returning sharks to be investigated and whale shark growth parameters to be estimated. My study represents the first growth parameters produced from a wild aggregation of free-swimming whale sharks.

5.1 Comparison of length measurement methods

The comparison of visual estimates, laser photogrammetry, and tape measurements in my study, revealed significant information about the accuracy and precision of each measurement method and therefore, the validity of their uses. Visual length estimates were found to overestimate smaller shark sizes and underestimate larger shark sizes compared to the other two measurement methods, which was also reported by Sequeira *et al.* (2016). Errors associated with visual estimates were found to be positively correlated with the size of the shark; as the total length of sharks increased so did the error when compared to the other two measurements methods. The visual measurements began to underestimate total length of sharks starting at 4 and 6 m compared to tape and laser measurements, respectively.

The accuracy of each measurement method is difficult to determine without direct comparison to the actual total length, a value never known for free-swimming animals. However, laser measurements are thought to be more accurate and precise compared to visual measurements (Rohner *et al.*, 2015; Sequeira *et al.*, 2016). Based on my findings, tape measurements provided similar total lengths and precision when compared to laser measurements and can be a useful tool when laser photogrammetry is not reliable or unavailable.

Realizing the inaccuracy of visual estimates has critical implications for understanding the demographics of whale sharks worldwide, as studies at most aggregation sites have utilized visual estimates, and thus may have underestimated the number of mature sharks present.

5.2 Average Sizes of New, Transient and Returning Sharks

New sharks were found to be significantly smaller than returning sharks. Small sharks are likely arriving to the South Ari Atoll where they stay and grow until they reach a certain size, possibly maturity (Pers. comm. R. Rees). The fact that some sharks have been documented in the South Ari Atoll for over ten years, coupled with few encounters of sharks within documented size at maturity, further supports this statement. Once large, or mature, they are likely fit enough to survive the patchy open ocean environment and may adopt a more pelagic lifestyle. Therefore, the South Ari Atoll may serve as a secondary nursery where juvenile sharks spend their years growing towards maturity (Heupel *et al.*, 2007). The absence of small neonates and mature adults in the South Ari Atoll further supports this hypothesis.

This has important management implications as the Maldives may serve as an important juvenile habitat, where whale sharks grow and mature before they leave the surrounding waters. Therefore, protecting these juvenile sharks is vital for the long-term survival of the species, at least in this region. The question of where these sharks are born before they make their way to the Maldives and where critical primary nursery areas are located remains unanswered.

Transient sharks were not significantly different in size from new and returning sharks. Perhaps these transient sharks would fit into one of the other occurrence categories and were not originally encountered when they first came to the area. Another possible scenario is that these transient sharks are philopatric to other areas of the Maldives. There are reports of whale sharks being seen at other atolls and certain whale sharks may show site fidelity and/or pass through the South Ari Atoll in their travels (Pers. comm. R. Rees).

5.3 Growth parameters

This is the first study to calculate growth parameters from measurements of free-swimming whale sharks. Rohner *et al.* (2015) aimed to calculate growth rates by using laser photogrammetry but found that laser measurements may not be suitable for measuring growth rates over short (1-3 year) periods. However, the largest temporal change in my study was seven years, with a mean of 3.16 years between measurements of individuals and therefore suitable to include laser photogrammetry.

When visual estimates were included in the analysis, it resulted in a very large L_∞ and had large chi square values. Visual estimates are useful in determining general approximation of whale shark sizes, however, they may not be useful in determining more specific parameters such as growth rates. This is likely due to the large error associated with visual measurements. Tape and laser measurements recorded over a long period of time were able to produce von Bertalanffy parameters and growth rates that were realistic and had much lower chi square values.

My combined sexes von Bertalanffy parameters ($L_\infty = 19.56, k = 0.021$) differ from the biannually deposited vertebral ring analysis of whale sharks from the Northwest Pacific for combined sexes utilizing a two parameter von Bertalanffy growth function (Hsu *et al.*, 2014). However, the parameters derived in my study are more in line with the biannual parameters of Hsu *et al.* (2014) when male and female sharks were analyzed separately using a two parameter von Bertalanffy growth equation. The L_∞ and k values for combined sexes of my study are also aligned with Wintner's (2000) study. Whale shark growth parameters from the referenced studies are summarized in Tables 6 and 7. The corresponding total length and growth rate related to ages are summarized in Tables 8 and 9.

The male only growth parameters derived from my study (L_∞ =18.08, k = 0.023) are slightly lower than the biannual vertebral ring deposition-based, male only growth parameters determined by Hsu *et al.* (2014). However, Hsu *et al.* (2014) could not rule out annual ring band pair formation when they were investigating vertebrae. My study yielded results more aligned with male growth parameters derived from annual band formation (L_∞=18.02, k=0.017) determined by Hsu *et al.* (2014).

The L_∞, determined in my study, is aligned with the largest sharks documented in the literature, which are summarized in Table 5. The largest specimen documented was recorded at 20.4 m by Compagno (2001). Similarly, Chen *et al.* (1997) observed a 20 m specimen from a Taiwanese fish market. However, Borrell *et al.* (2011), McClain *et al.* (2015), and Eckert and Stewart (2001) all recorded maximum total lengths (18-18.8 m) that are consistent with my combined sexes L_∞.

My study determined a k value of 0.02 for both combined sexes and males only. The growth coefficient k describes the rate at which an individual reaches maximum size from its birth size. There are large ranges of k among chondricthyans and these vary by species and life history (Goldman *et al.*, 2012). There are a few shark species that have a k value less than 0.1 and these low values appear to be associated with large migratory species, such as the whale shark, in which energy may be used primarily for movement more than growth (Hsu *et al.*, 2014).

My study documented a growth rate primarily from juvenile sharks that began at ~40 cm/yr after birth and declined to ~26 cm/yr by age 20. The large range of growth rates in wild free-swimming whale sharks is likely a result of large error margins associated with the measurement (Holmberg *et al.*, 2009). However, growth rates in aquaria are likely higher than wild growth rates due to lower energy demands, constant temperature, availability of food and other aspects (Mohan *et al.*, 2004). Growth rates may also differ between sexes, size classes and geographic location. Growth rates in aquaria showed that neonatal pups grew faster than juvenile whale sharks and that juvenile sharks showed variable growth rates with females growing faster than males (Rowat and Brooks, 2012, Uchida *et al.*, 2000, Chang *et al.*, 1997). Females may exhibit different growth rates and small individuals may grow much faster than the sharks in my study. There is a paucity of information concerning small whale sharks and only 19 sharks <1.5 m have been recorded (Bradshaw and Brooks, 2012). Information about newborn and small whale shark is lacking and this size class may demonstrate a different growth rate than the one derived from the immature males in my study.

The growth parameters determined in my study are consistent with those values produced from other age and growth studies utilizing vertebral analysis (Hsu *et al.*, 2014, Wintner, 2000). This further provides validity and support to the methods utilized in my study.

5.4 Age at Maturity and Longevity

A male age at maturity of ~25 years and a longevity of ~140 years determined by my study make the whale shark very susceptible to any level of exploitation or population decrease. Longevity of whale sharks has been thought to be greater than 100 years (Pauly, 1997; Bradshaw *et al.*, 2007) and my study yielded a similar longevity to an extrapolated longevity from one of Wintner's (2000) von Bertalanffy growth equations pf ~140 years (Table 6).

Table 5: Summary of the largest size whale sharks observed and documented in the literature.

Total Length (m)	References
18.8	Northwestern Indian Ocean (Borrell *et al.*, 2011; McClain *et al.*, 2015)
18	Sea of Cortez (Eckert and Stewart, 2001)
20	Taiwan (Chen, Lin and Joung, 1997)
21.4	(Compagno, 2001)
19.56	My Study (Combined Sexes)
18.08	My Study (Males)

Table 6: Summary of age and growth parameters of whale sharks derived from growth models. T_{max} was calculated utilizing an L_0 of 0.64 m.

$L_\infty(m)$	k (yr^{-1})	t_{max} (years)	Method	Location
19.56	0.021	142.5	Free-swimming (N=44) (Combined Sexes)	South Ari Atoll, Maldives
18.08	0.023	135.14	Free-Swimming (N=40) (Males)	South Ari, Atoll, Maldives
16.8	0.037	89.53	Vertebrae (biannual rings) (Combined Sexes; N=95)	Northwest Pacific (Hsu *et al.*, 2014)
19.7	0.03	99.74	Vertebrae (biannual rings) (Males; N=44)	Northwest Pacific (Hsu *et al.*, 2014)
20.5	0.029	103.91	Vertebrae (biannual rings) (Females; N=31)	Northwest Pacific (Hsu *et al.*, 2014)
15.34	0.021	166.84	Vertebrae (annual rings) (Combined Sexes; N=95)	Northwest Pacific (Hsu *et al.*, 2014)
14.96	0.032	111.19 (extrapolated)	Vertebrae (Combined Sexes; N=15)	South Africa (Wintner 2000)
19.66	0.021	142.69 (extrapolated)	Vertebrae (Combined Sexes; N=15)	South Africa (Wintner 2000)
14	0.03	123.44 (extrapolated)		(Pauly 1997)

Table 7: Summary of documented growth rates observed from live individuals (Rowat and Brooks, 2012). Sexes: UK for unknown, M for males, F for females.

Sex	*Habitat*	*Method*	*Initial TL (m)*	*End TL (m)*	*Growth Rate (cm year^{-1})*	*Source*
UK	Aquarium	Tape (Direct)	0.6	1.4	240.3	1
M	Aquarium	Tape (Direct)	0.6	3.7	97.8	2
F	Aquarium	Tape (Direct)	4.07	6.3	45.2	3
F	Aquarium	Tape (Direct)	3.65	5.3	29.5	4
M	Aquarium	Tape (Direct)	4.5	5.1	21.6	4
M	Aquarium	Tape (Direct)	4.85	5.2	25.5	4
F	Aquarium	Tape (Direct)	7.62		33	5
F	Aquarium	Tape (Direct)	7.87		37	5
M	Aquarium	Tape (Direct)	4.6	7.44	28 – 12.5	5
UK	Wild	Visual (Estimated)			3-70	6
UK	Wild	Visual (Estimated)			8-82	7
Combined	Wild	Tape and Laser	0.64	19.56	39.5	My study
M	Wild	Tape and Laser	0.64	18.08	40.3	My Study

[1]Chang *et al.* 1997; [2]Nishida, 2001; [3]Kitafuji and Yamamoto, 1998; [4]Uchida *et al.*, 2000; [5]Sato *et al.*, 2016; [6]Graham and Roberts, 2007; [7]Riley *et al.*, 2010.

Table 8: Growth rates from the combined sexes growth parameters derived from vertebral analysis by each study to determine age and growth.

	Combined Sexes					
	My Study	Wintner (2000)		Hsu *et al.* (2014) Biannual	Hsu *et al.* (2014) Annual	Pauly (1997)
Age (yr)	**Growth Rates (m/yr)**					
0	--	--	--	--	--	--
1	0.395	0.400	0.444	0.603	0.280	0.398
2	0.387	0.392	0.430	0.580	0.275	0.386
3	0.379	0.383	0.417	0.558	0.270	0.374
4	0.371	0.375	0.403	0.537	0.265	0.363
5	0.363	0.368	0.391	0.516	0.261	0.353
6	0.355	0.360	0.378	0.497	0.256	0.342
7	0.348	0.352	0.366	0.478	0.252	0.332
8	0.341	0.345	0.355	0.460	0.248	0.322
9	0.334	0.338	0.344	0.443	0.243	0.313
10	0.327	0.331	0.333	0.426	0.239	0.303
11	0.320	0.324	0.322	0.410	0.235	0.294
12	0.313	0.317	0.312	0.394	0.231	0.286
13	0.307	0.311	0.302	0.379	0.227	0.277
14	0.300	0.304	0.293	0.365	0.223	0.269
15	0.294	0.298	0.284	0.351	0.219	0.261
16	0.288	0.292	0.275	0.338	0.215	0.253
17	0.282	0.286	0.266	0.325	0.212	0.246
18	0.276	0.280	0.258	0.313	0.208	0.239
19	0.270	0.274	0.250	0.301	0.204	0.232
20	0.265	0.268	0.242	0.289	0.201	0.225

Table 9: Total lengths from the combined sexes growth equations derived from vertebral analysis by each study to determine age and growth.

	Combined Sexes					
	My Study	Wintner (2000)		Hsu *et al.* (2014) Biannual	Hsu *et al.* (2014) Annual	Pauly (1997)
Age (yr)	**Total Length (m)**					
0	0.640	0.421	0.401	0.640	0.640	0.550
1	1.035	0.820	0.860	1.224	0.950	0.948
2	1.422	1.212	1.304	1.787	1.253	1.333
3	1.800	1.595	1.734	2.329	1.550	1.708
4	2.171	1.971	2.151	2.852	1.840	2.071
5	2.534	2.338	2.554	3.356	2.125	2.423
6	2.889	2.698	2.954	3.842	2.403	2.766
7	3.237	3.051	3.323	4.310	2.676	3.098
8	3.578	3.396	3.690	4.762	2.943	3.420
9	3.912	3..734	4.045	5.197	3.204	3.733
10	4.238	4.065	4.388	5.616	3.460	4.036
11	4.558	4.389	4.721	6.020	3.710	4.330
12	4.871	4.706	5.044	6.410	3.955	4.616
13	5.178	5.017	5.356	6.785	4.195	4.894
14	5.478	5.321	5.658	7.147	4.430	5.163
15	5.772	5.619	5.951	7.496	4.660	5.424
16	6.060	5.911	6.235	7.832	4.885	5.677
17	6.342	6.197	6.510	8.157	5.105	5.923
18	6.617	6.477	6.776	8.469	5.321	6.162
19	6.888	6.751	7.034	8.770	5.532	6.394
20	7.152	7.019	7.283	9.060	5.739	6.618

Table 10: Growth rates from the male growth parameters produced in my study and biannual and annual band formation derived from Hsu et al. (2014).

	Males		
	My Study	Hsu *et al.* (2014) Biannual Rings	Hsu *et al.* (2014) Annual Rings
Age (yr)	**Growth Rates (m/yr)**		
0	--	--	--
1	0.403	0.563	0.293
2	0.394	0.547	0.288
3	0.385	0.531	0.283
4	0.376	0.515	0.278
5	0.367	0.500	0.274
6	0.359	0.485	0.269
7	0.351	0.471	0.265
8	0.342	0.457	0.260
9	0.335	0.443	0.256
10	0.327	0.430	0.251
11	0.319	0.417	0.247
12	0.312	0.405	0.243
13	0.305	0.393	0.239
14	0.298	0.381	0.235
15	0.291	0.370	0.231
16	0.284	0.359	0.227
17	0.277	0.349	0.223
18	0.271	0.338	0.219
19	0.265	0.328	0.216
20	0.259	0.319	0.212

6. Conclusions

My study found a similar bias as Sequeira *et al.* (2016) where visual estimates are underestimating total lengths of whale sharks. This confirms the concern that the sizes of large whale sharks may be questionable in the literature. There may actually be larger sharks, than previously thought, appearing at aggregation sites worldwide, where visual size estimates dominate.

The significant differences between the label of sharks throughout the years of my study lends some, albeit circumstantial, support to the theory that small juvenile whale sharks arrive at the Maldives and stay until they reach a certain size or maturity. The largest sharks in my study were 8.9 m and immature, but within the range of documented size at maturity. No sharks larger than 8.9 m have been encountered and this may be due to the fact that the South Ari Atoll, Maldives is a suitable habitat for juvenile whale sharks but not suitable for larger mature individuals.

The growth rates determined in my study are derived from the juvenile male dominated population in the Maldives. However, growth rates may vary by geographic region and aggregation site. Sharks encountered at other aggregation sites may experience different environmental conditions and stressors that could positively or negatively affect growth rates. For example, 69 % of the sharks seen in the SAMPA have a documented injury with 78 % of these injuries classified as anthropogenic. These injuries may have an effect on the growth rates of whale sharks as resources and energy contribute to the healing of the injury and not necessarily the growth of the animal. Speed *et al.* (2008) found similar percentages of injuries at other aggregation sites in the Indian Ocean. This may slow the growth of whale sharks in the Maldives and affect the L_∞ and k values that were generated in my study.

Growth rates in wild populations have shown larger ranges and are likely the result of errors in measurement methods. Utilizing more reliable measurement methods (tape and laser) in my study allowed for a more accurate representation of growth rates in the wild**.** My L_∞ and k value for combined sexes are consistent with the literature and are the first growth parameters defined from an aggregation of free-swimming whale sharks.

The results of my study have important implications for management of whale sharks worldwide. Large maximum sizes, slow growth and long lifespans mean that any negative impact on whale sharks can cause serious declines in populations. The Maldives was one of the first countries to ban its whale shark fisheries in 1995 (Cagua *et al.*, 2014). However, directed fisheries for whale sharks still occurred in surrounding waters, with Taiwan being the last country to ban its fisheries in 2007 (Hsu *et al.*, 2012). In my conversations with veteran whale shark fishermen, they have indicated that total lengths of sharks caught in the past were much larger than the sizes of sharks seen via tourism today in the Maldives. They also reported more encounters with multiple sharks at a time, which is now infrequent within this aggregation site, as personally observed. Sequeira *et al.* (2016) found that large whale sharks were recorded in datasets around the world prior to 2006. Late maturation, long lifespans and slow growth may mean that it will take many years to recover from these declines as whale shark populations have decreased by up to 63% in the Indo-Pacific (Pierce and Norman, 2016). Therefore, international management and conservation measures need to be implemented to help protect whale sharks worldwide.

It is important to understand how the Maldivian aggregation fits globally into whale shark populations. There has been little to no whale shark connectivity at different aggregation sites in the Indian Ocean with the exception of one individual which was seen in Mozambique and later encountered in the Seychelles after 8 months; a distance of 3000 km over 221 days (Andrzejaczek *et al.,* 2016). Also, the average sizes of sharks at important coastal aggregation sites worldwide are smaller than the documented sizes at maturity (Rohner *et al.*, 2015). This may mean that globally, coastal sites are suitable for juvenile sharks and this bias of coastal aggregation sites may suggest that mature and newborn whale sharks are utilizing a different habitat (Rohner *et al.,* 2015). This also raises the question as to where newborn, female and mature sharks are worldwide (Rohner *et al.,* 2015).

Once whale sharks reach maturity they may spend more time in the open ocean. Ramirez-Macias *et al.* (2012) looked at whale sharks both inshore and offshore the Gulf of California and found that juvenile sharks were regularly seen inshore while larger mature individuals were seen offshore. This may mean that further studies conducted offshore are necessary in order to understand the ecology of mature whale sharks. Sharks that are close to size at maturity in the Maldives could also be tagged in order to see if and/or where they travel to once they leave the area. This could paint a better picture as to how whale sharks utilize the Indo-Pacific in their movements and provide insight into potential mating interactions and habitat usage for mature individuals.

One of the greatest challenges to conservation of whale sharks is the poor understanding of important life history characteristics (Pravin, 2000). A more thorough grasp of age and growth parameters will lead to better estimates of the ability for whale shark populations to be able to grow and recover from overexploitation. Furthermore, better knowledge of age at maturity and longevity is vital for effective management plans (Goldman *et al.*, 2012). Utilizing more precise and accurate methods to determine life history parameters is necessary in order to determine population status. Increased awareness of whale shark demographics at other aggregation sites will provide important answers to these questions. It is necessary that more accurate measurement techniques are used at aggregation sites worldwide to aid in the understanding of whale shark age and growth in wild populations.

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9. Appendix A. Data sheet used to collect information from each whale shark encounter

Big Fish Network Encounter Sheet

Name of Researcher:	<u>Date:</u>	Time Start Searching:	Time Stop Searching:	Breaks (Hrs):	Encounter Number: ________of________

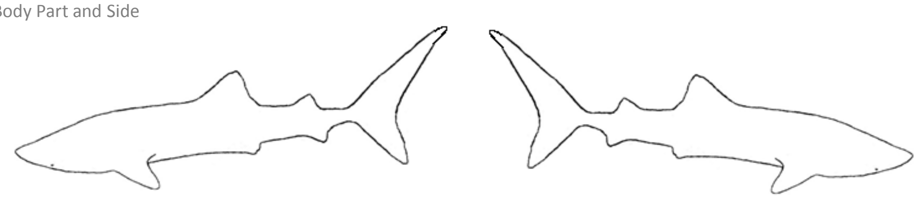
Time Encounter:	Encounter Duration:	Location:	Coordinates North:	Coordinates East:

Whale Shark ID if Known:	Est Length To 0.5m:	Sex:

Swim Direction:	Behaviour:	Other Wildlife:	Persons start:	Persons Max:	Boats Start:	Boats Max:	Distance to closest boat:

Distinguishing feature:	Injury Type:	Severity:

Body Part and Side



Reef depth:	Sea Temp:	Wind Direction:	Wind Speed:	Cloud Cover:	Sea State:	Current Direction:	Current Strength:	Visibility:

Notes

MALDIVES WHALESHARK RESEARCH PROGRAMME

OFFICIAL PARTNER BIG FISH NETWORK