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

By

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Abstract

Despite the growing number of interactions with whale sharks through ecotourism, little or no information is available on important aspects of whale shark biology, such as growth rates, reproductive rates, survival rates and breeding habitats (Holmberg *et al.*, 2009). Critical information, such as age and growth of whale sharks, is needed to improve the management and conservation of the species (Hsu *et al.*, 2014; Rohner *et al.*, 2015). Accurate measurement of life-history parameters can improve demographic models for whale sharks and enable better evaluation of their vulnerability to fishing pressures and recovery from population declines (Rohner *et al.*, 2015). For the Maldives, knowledge on the ages and sizes of whale sharks may also provide crucial information into migration routes and potential links between other Indian Ocean aggregation sites.

This study aimed to expand on the knowledge of age and growth of whale sharks in the Maldives by calculating growth parameters and rates from encounters during the time period of April 2006 to May 2016. A total of 1545 encounters with 125 individual sharks were recorded during this time period. Total length estimates were taken via three different measurement methods (visual, tape, and laser) and linear regression was utilized to investigate how the different methods were related to one another. This study showed that visual estimates tended to underestimate large sharks and tape and laser measurements yielded similar results to one another ($R^2 = 0.824$). New sharks to the South Ari Atoll were significantly smaller than returning sharks. This provides evidence that small sharks may be recruited to the South Ari Atoll, where they stay and grow until they reach maturity and then they leave the area.

This study was the first of its kind to produce growth parameters and rates from measurements of free-swimming whale sharks. Growth parameters for combined sex, calculated from 180 encounters with 44 individual sharks (3.16m – 8.00m), yielded an L_∞ of 19.556m and a k value of 0.0211yr^{-1}. Analyzing 177 encounters with 40 male sharks (3.16m-8.00m) changed these parameters to an L_∞ of 18.081m and a k value of 0.0234yr^{1}. This corresponds to a male age of maturity of ~25 years and a longevity of ~140 years.

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 18.8m 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 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 1928m (Tyminski *et al.*, 2015; Thums *et al.*, 2012). They exhibit slow growth, late maturation and long lifespans, which make them susceptible to all levels of exploitation (Compagno, 2001). As of June 2016, 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, 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 size (Jeffreys *et al.*, 2013). There is a paucity of information on whale shark reproduction and pupping, as well as breeding and pupping locations (Holmberg *et al.*, 2009). Age of maturity is poorly understood in whale sharks as well as gestation period and number of pups produced in a female's lifetime. These factors are vital for the management and conservation of a species. The majority of coastal whale shark aggregation sites are comprised of immature males and there is a lack of information on where female whale sharks are located. This may have implications of habitat selection between the sexes. Whale shark migration is also poorly understood and there have been no major linkages between whale shark aggregation sites.

One way to answer some of these questions is to focus on areas where whale sharks form aggregations worldwide. Many of these aggregations are seasonal and occur in different locations around the world in response to local increases in food availability linked to certain spawning events of prey species (Heyman *et al.*, 2001). These aggregations, which often have no more than a few hundred sharks, are beginning to be 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 movement dynamics. Aggregation sites can lead researchers to where whale sharks are located and the identification of individual whale sharks can generate important information. Whale sharks have unique pigmentation comprised of many lines and spots. This natural patterning does not change throughout their lifetime and is useful for photo identification of individuals (Norman, 1999). These digital "fingerprints" can be used to track individual whale sharks over wide geographic areas and time spans (Arzoumanian *et al.*, 2005). Population dynamics and growth rates can also be studied via the identification of individual whale sharks.

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 a better understanding of age at maturity, lifespan and mortality. These parameters are crucial in determining population sizes and status of the species. There have only been a few age and growth parameters derived from vertebral rings to determine age and growth. Hsu *et al.* (2014) analyzed vertebrae from the North-west Pacific and found an L_∞ of 16.8m 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 14.96m and a k value of 0.021 and 0.032, respectively. Pauly (1997) stated tentative values of an L_∞ of 14m and a k value of 0.03. However, precise age and growth has never been derived from free-swimming whale sharks. It is also important to note that while there are no genetically differentiated populations of whale sharks in the Indian Ocean, there have been no confirmed movements of animals between the Eastern and Western Indian Ocean populations (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.

When establishing 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 measure total length of free-swimming whale sharks: visual, tape and laser. A visual estimate is obtained by averaging the total length estimated by two or more researchers. A tape measure estimate is obtained when two researchers swim down and record the total length by stretching a tape measure above the shark from the mouth to the caudal fin (this is repeated multiple times for more accurate measurements). A laser estimate, or laser photogrammetry, is conducted through the use of two lasers set 50 cm apart from each other. This method is based on the principle that parallel lasers project light an equal distant apart from the origin (Rohner *et al.*, 2011). A photograph is taken of the shark with the two laser points visible, which act as a scale bar. The length from the 5th gill to the start of the first dorsal fin is recorded as well as the number of pixels per 50 cm. Rohner *et al.* (2011) derived a formula to calculate total length of whale sharks from laser photogrammetry. Total length is calculated through the following formula:

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

Some challenges present themselves in the methods used to estimate total length and comparison of the methods used to measure whale sharks is important for the understanding of total lengths recorded. Visual estimates are the easiest and most convenient method to utilize while in the field. However, if visual estimates are not accurate then this creates problems with data collection and analysis. Comparing visual estimates against more accurate methods, *i.e* tape and laser, provided analysis into how accurate visual estimates are to determine total length. Human spatial perception is biased underwater and encounters can be very quick. Therefore, visual total length estimates will likely include significant error even when made by experienced researchers and minimum standard error is thought to be 0.5m (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 the accuracy of whale shark size estimates and to greatly reduce the error associated with visual estimates (Rohner et al., 2015). The equipment needed to carry out laser photogrammetry is simple and allows a single researcher to collect a large number of measurements on a single target. Paired-laser photogrammetry uses two parallel lasers, mounted with a camera in the center, to project two points of light onto a target that show a scale of known length to infer the size of the target. However, non-parallel alignment of the laser pointers will cause the scale to change between the laser points depending on the distance from the target. Paired-laser photogrammetry is based on the principle that laser will project light equidistant apart from the origin. Laser pointers that are not mounted correctly or that become misaligned during use will create inaccurate measurements and lead to incorrect size estimates. Parallax error can be another significant source of error while using paired-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). 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.

Tape measurements are recorded when sharks are within freediving range of the researchers (Figure 1). One researcher holds the start of the tape measure and swims down above the head of the whale shark. The second researcher swims down above the caudal fin of the whale shark. The first researcher gives one sharp pull when they are in position at the anterior of the whale shark. The second researcher then removes all the slack in the line and gives two sharp pulls when they have recorded the measurement. This procedure is done multiple times and the measurements are averaged to improve accuracy. 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 is higher or lower than the other, this can create errors in the measurement. Repeating the measurements during an encounter helps to reduce these errors in collecting an accurate total length of the shark. However, appropriate positioning can be confirmed from photographs taken during encounters where sharks were measured. A slack tape measure will also produce error while recording the total length of a whale shark. A tape measurement where the slack is not removed from the line can overestimate the shark. The second researcher has to ensure that the slack is removed from the line before they record the measurement. This can provide a more accurate measurement of a whale shark's total length.

Understanding the differences in total length derived by each method is important for their use in subsequent data analysis and interpretation of data sets from different regions or years which used different size estimation methods. 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.

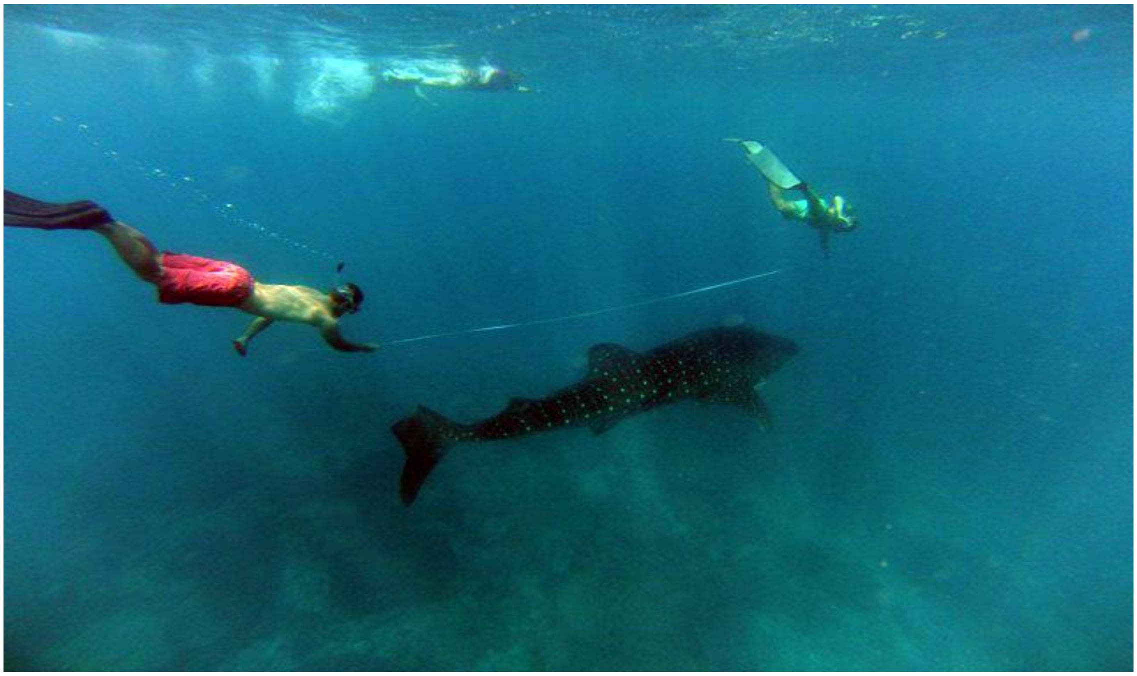

Figure 1: Tape measurement method used to determine total length

One aggregation site that could provide more information into whale shark age and growth is the South Ari Atoll, Maldives. Whale sharks occur year-round in the South Ari Atoll and the Maldives Whale Shark Research Programme (MWSRP) have been collecting data on this aggregation for over ten years (Cagua *et al.*, 2014). Identification of individual whale sharks coupled with encounter data spanning ten years can help provide answers into age and growth of free-swimming whale sharks. The reason(s) why whale sharks are seen in the Maldives year-round while other aggregation sites are seasonal is still unknown. In order to better 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 for a better understanding of the sizes and ages of sharks that stay in the area or pass through the area. 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 in the Maldives may be year-round or permanent residents of the archipelago (Riley *et al.*, 2010). However, more data is needed to confirm this theory.

In order to investigate age and growth there needs to be an analysis into the methods used to determine total length. The assessment of measurement methods' accuracy will improve the estimates of the age and sizes of whale sharks in the Maldives and allow for the standardization of data. As a result, there will be a better opportunity to determine age of maturity, lifespan, mortality and population size of the whale sharks in the Maldives. Preliminary research into growth rates of whale sharks in the Maldives from 2006 through 2008 suggested a (total length) growth rate of 0.45m yr^{-1} (n=13, Riley *et al.*, 2010). This rate is relatively similar to rates obtained from the analysis of vertebrae from whale sharks in the Northwest Pacific, specifically 0.60m yr^{-1} that slowly declined to 0.29m yr^{-1} by age twenty (Hsu *et al.*, 2014). Pauly (1997) suggested a growth rate of 0.398 m yr^{-1} that declined to 0.225 m yr^{-1} by age 20. However, there has not been accurate values of age and growth determined from free-swimming whale sharks and most age and growth data comes from observation in aquaria of vertebral analysis. The comparison of growth rates between locations would be important to understand the population dynamics of this species.

2. Objectives

The objectives of this study were to: (1) assess relative accuracy of different methods of measurement; (2) determine size differences between new, transient and returning sharks at South Ari Atoll, Maldives; (3) determine the growth rate of the whale shark population in the Maldives and compare them to published growth rates in the literature for other regions, such as the Northwest Pacific as documented in Hsu *et al.* (2014).

3. Methods

3.1 Study Area

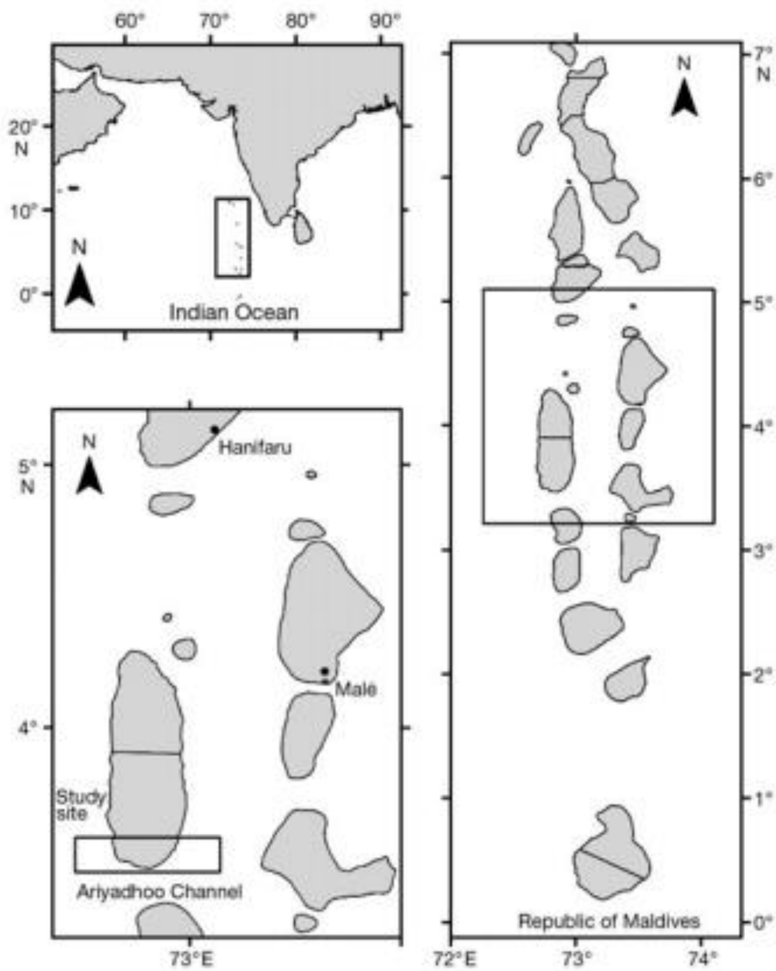

Figure 2: South Ari Atoll, Maldives (Riley *et al.*, 2010)

The study area was located in the South Ari Atoll in the Republic of the Maldives (Figure 2). The South Ari Marine Protected Area (SAMPA), designated in 2009, is the largest MPA in the Maldives with a total area of 42km^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. The SAMPA is approximately 105km southwest of Malé, the capital city of the Republic of the Maldives (Riley *et al.*, 2010).

3.2 Study Population

A whale shark population from the South Ari Atoll, Maldives was studied. This is a unique whale shark aggregation site because whale sharks are encountered year-round, whereas other aggregation sites are seasonal in nature (Cagua *et al.*, 2014, Rowat, 2007). The Maldives Whale Shark Research Programme have been studying whale sharks in the South Ari Atoll, Maldives since 2006 and have accumulated an extensive data set on this aggregation's size dynamic. To date 295 individual sharks have been identified with many re-sightings of the same individuals.

3.3 Surveys

Surveys followed the protocol described by Riley *et al.* (2010) to locate whale sharks along the South Ari MPA. When a shark was spotted, researchers were dropped 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 can be seen in Appendix A. Total length was measured utilizing all three methods whenever feasible. Identification photographs were taken during the encounters and were later analyzed on land. A pattern recognition software (I^3S, Interactive Individual Identification System http://reijins.com/i3s) described in Brooks *et al.* (2010) was used to find matches between the photographs and sharks in the database. Capture-mark-recapture methods are useful for collecting data about a species over a long period of time. Once a shark is uniquely identified, then re-sightings in following years can help provide detailed information about age and growth parameters.

3.3.1 Visual Estimates

Total length visual estimates were made after every encounter. Experienced researchers estimated to the nearest 0.5m the total length of the shark encountered. Two or more researchers stated their estimates and the average was documented in the dataset.

3.3.2 Laser Estimates

Laser estimates were made by utilizing a rig with two lasers set 50cm apart and a camera mounted in the center. Two green underwater Apinex (BALP-LG05-B150) laser pointers and an Olympus Tough TG 4 camera created the laser rig. These lasers projected two laser points that were visible on the shark when photo identification photographs were taken. Utilizing the fact that the lasers are a set distance apart can allow for an interpretation of the total length of the shark. Rohner *et al.* (2011) provided calculations to determine total length from laser photographs and these values ~~were recorded~~were recorded in the data. Laser photographs were taken during the encounter and later calculated back on land.

Figure 3: Laser measurement method used to determine total length

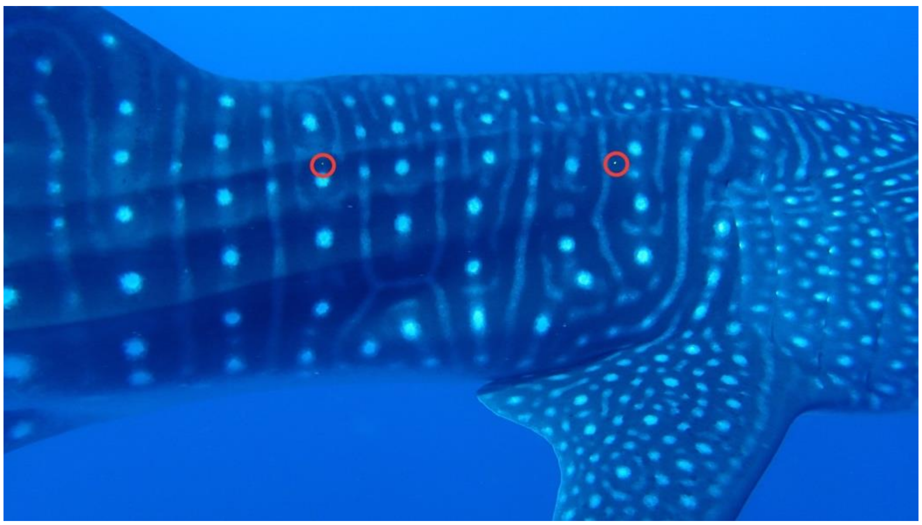

Figure 4: Identification photograph taken with laser points visible used to determine total length of whale sharks

3.3.3 Tape Estimates

Tape estimates were made whenever feasible during an encounter. This method involved two researchers diving down above the shark to measure the dorsal side, from the tip of the mouth to the end of the caudal fin. One researcher swam down with the tape and kept it in line with the tip of the mouth. The other researcher swam down 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.

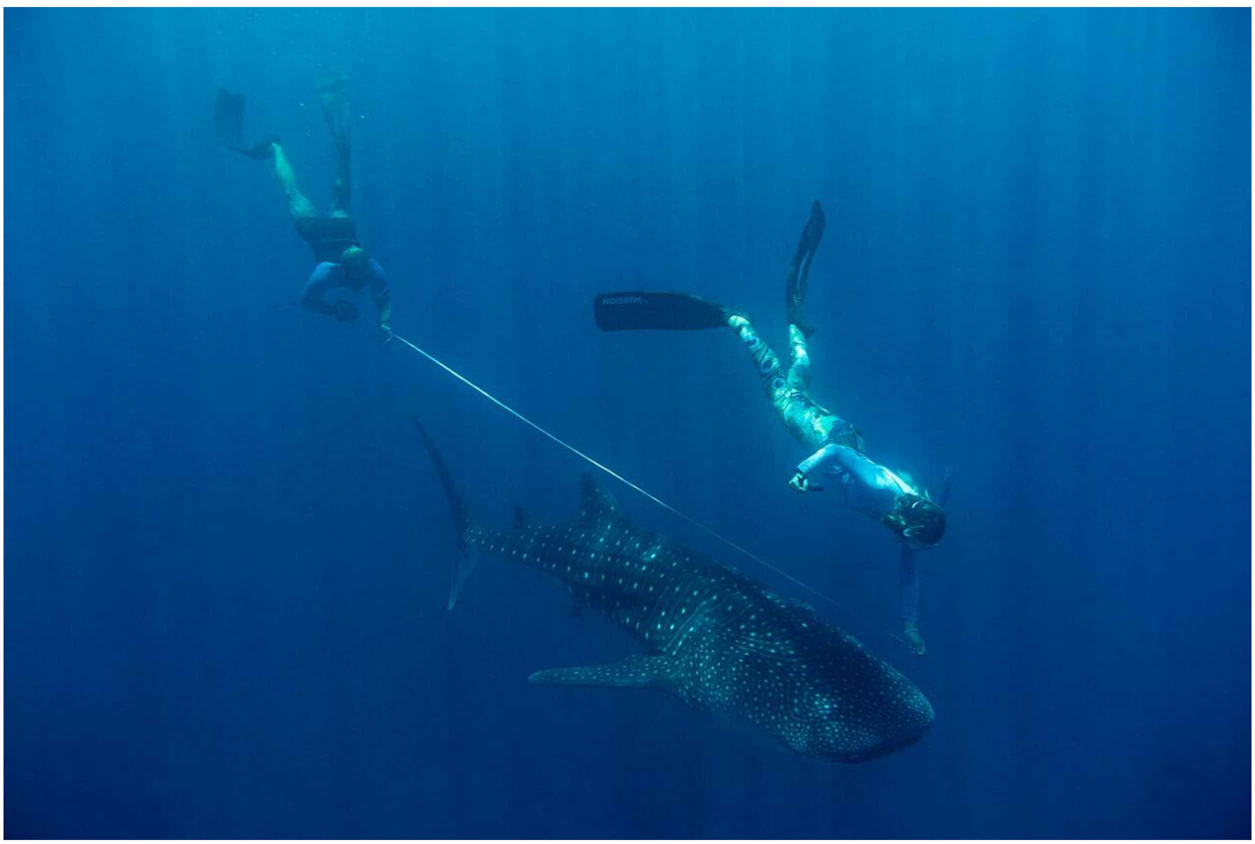

Figure 5: Tape measurement method used to determine total length

3*.3.4 Photo Identification*

Photo identification was done on land after the day's survey was concluded. Whale sharks have body pigmentation patterns that are unique to each shark and allows for identification of individual sharks. 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^3S, Interactive Individual Identification System) was used to determine matches among photographs and the database (Riley *et al.*, 2010). First, reference points were selected in I^3S. Reference point 1 was the top of the 5th gill, point 2 was where the pectoral fin intersects with the body and point 3 was the bottom of the 5th gill. Once these reference points were defined then white spots were selected to identify the shark. At least 12 spots were needed in order to identify the shark. The photograph was then run through an algorithm that provided the closest match from known sharks in the database. I^3S showed the top matches from the database to the shark being identified. Successful matches were visually confirmed to prevent any errors.

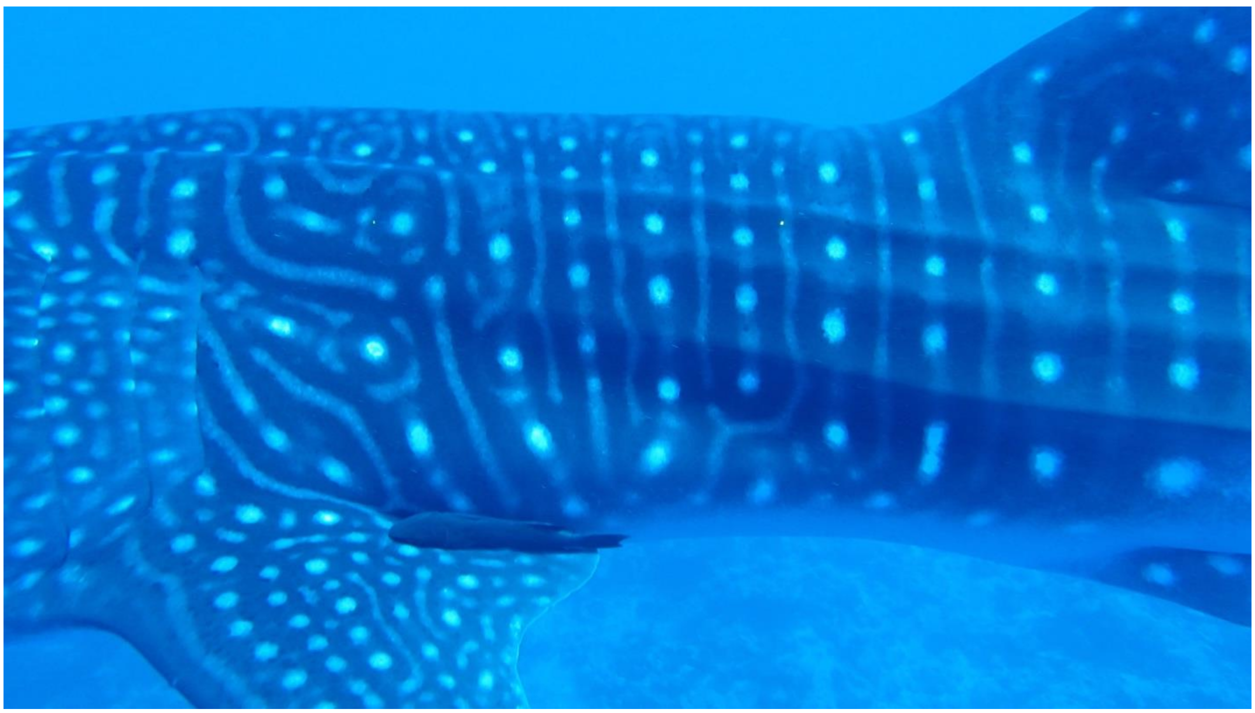

Figure 6: Identification photograph.

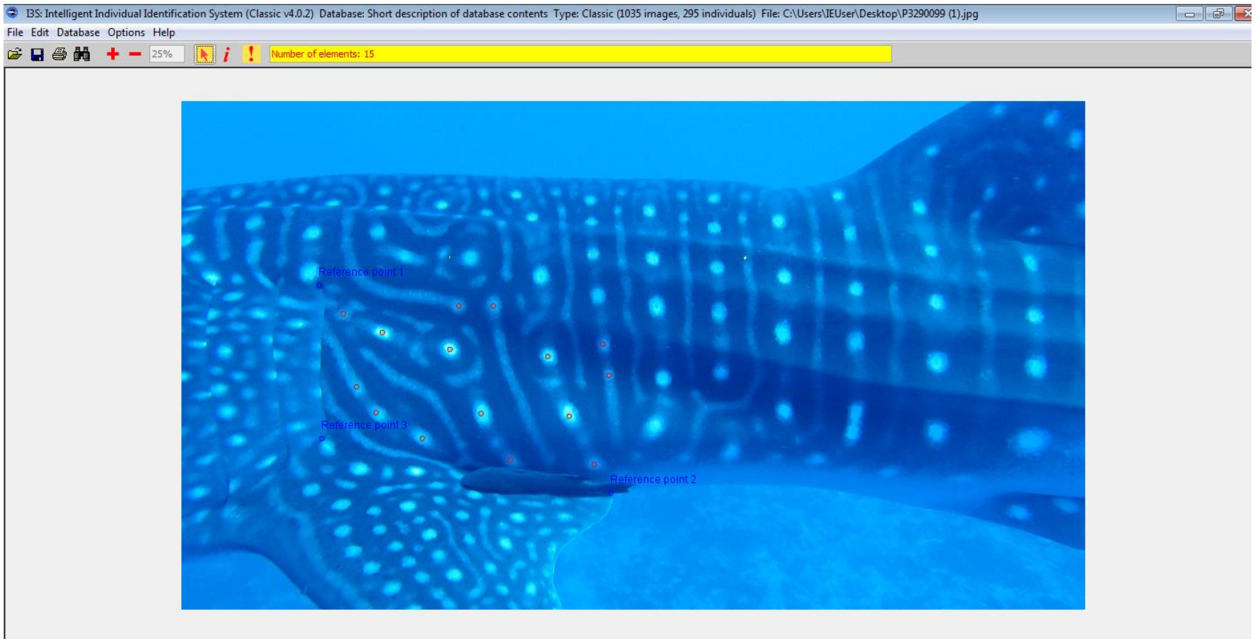

Figure 7: Identification photograph in I^{3}S with reference points and spots selected.

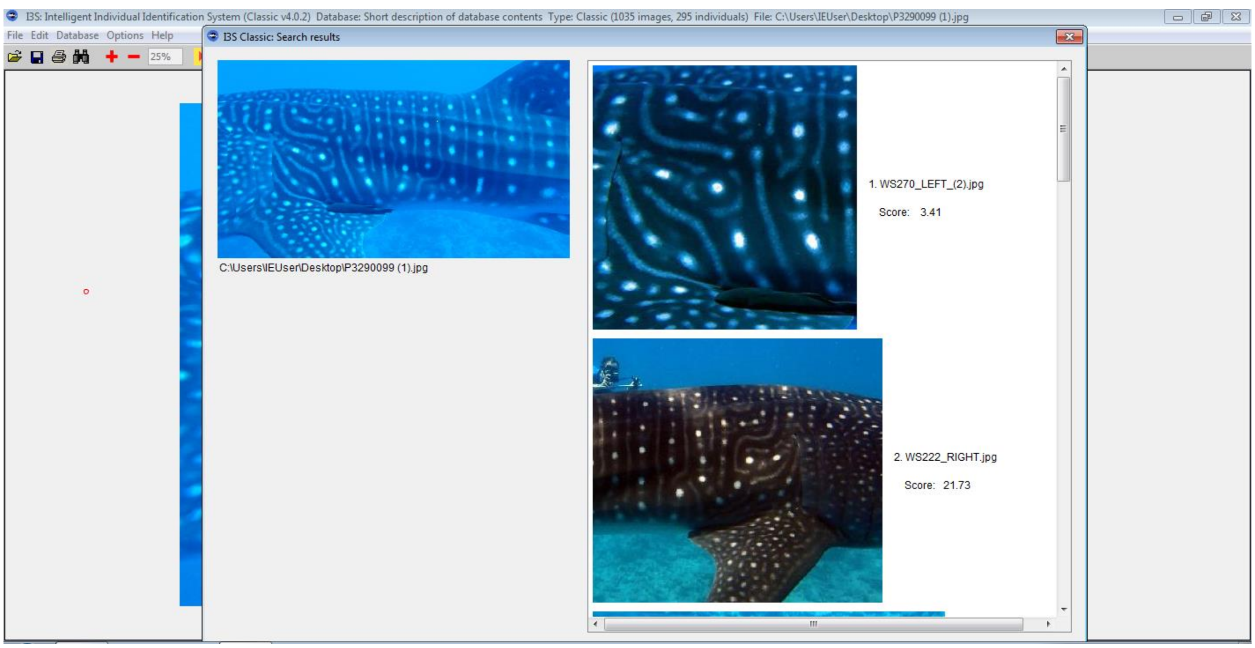

Figure 8: Match of identification photograph and the corresponding photographs in the database

3.3.5 Sex Determination

Sex was determined by 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.

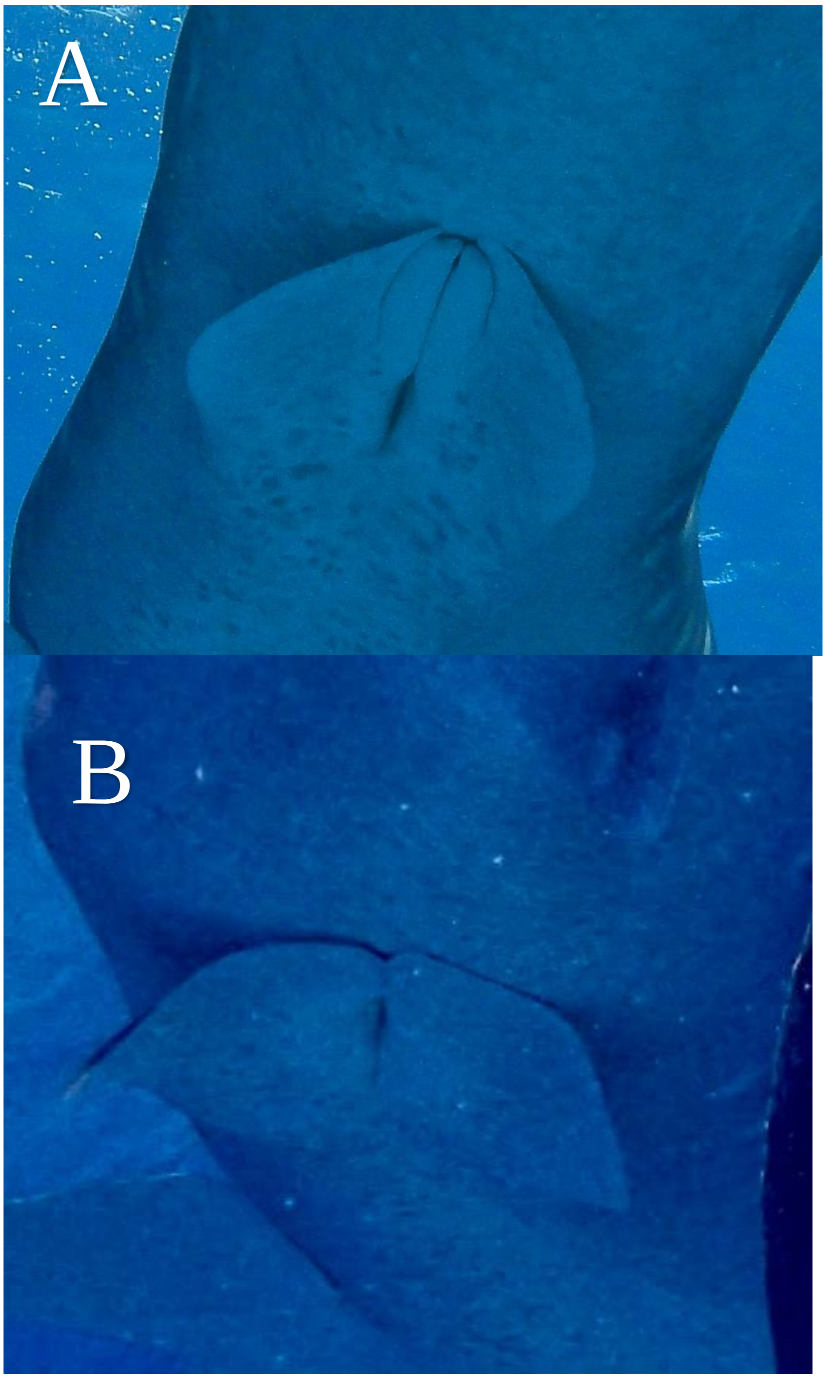

Figure 9: Sex determination. Males are identified by the presence of two external organs, called claspers (A). Females are identified by the absence of these organs (B)

3.4 Statistical Analyses

3.4.1 Regression Analysis

All statistical analyses were performed using R Studio. Growth rates and size trends were only analyzed after total length is converted into a uniform measurement. Each measurement method was compared in order to determine how they related to one another. Three regression plots were created by plotting each method against each other to determine the bias of each method 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 measurement. The variance of each encounter was calculated by subtracting the measurement recorded from the mean of the measurements. The square root of variance was then calculated to provide standard deviations for each measurement.

3.4.3 Differences between New, Transient and Returning Sharks

In the early years of the data collection each shark encountered was theoretically a new shark and would therefore skew proper labeling of each shark. To avoid mislabeling, we only considered labeling sharks after the number of new sharks seen per search effort remained constant. There were a total of 16 new sharks seen in 2006, the first year of study, and these served as a baseline for analysis of subsequent years. Sharks that were at liberty for at least a year were labeled new at the first encounter and returning for every subsequent encounter. Sharks that were only seen once within a year were labeled as transient (Fox *et al.*, 2013). All total length estimates were converted to an adjusted tape measurement. A histogram and an Analysis of Variance (ANOVA) were run to compare the average sizes of sharks by label per year. A Tukey Post Hoc test was run to determine what would influence the differences in sizes.

3.4.4 Growth parameters

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 altered growth rates. Laser measurements were converted to tape measurements due to lower variance and error of converting to a different measurement method. This was done to standardize the dataset. Tape and laser measurements that were recorded within the same month were averaged together to further reduce error associated with the measurements. Growth parameters were only calculated for sharks that were at liberty for at least a year because any small change in size accompanied by a small change in time quickly yields unrealistic growth rates. Since the age of the animals is 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, L_i is the capture size, k is the growth coefficient and Δt is the change in time (yrs) (Quinn and Deriso, 1999; Hart and Chute, 2009). Combined sex 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 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. Insufficient sample size, of small and large individuals, can often cause poor estimates of parameters using the von Bertalanffy growth equation (Tanaka, Calliet and Yudin, 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 equation 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 appears to be wide range of total lengths at birth (L_0) with Aca and Schmidt (2011) describing a 0.46m fully viable newborn whale shark. A 0.94m specimen was found in India with an external yolk sac attached, indicating that is was not at full term (Manojkumar, 2003). This study used an L_0 of 0.64m as this was the largest full term embryo from Joung *et al.* (1996). The authors divided whale shark embryos into three size classes, the largest (0.54-0.64m) were free of their egg cases, had their yolk sacs absorbed and appeared ready to be birthed (Stevens, 2007). Therefore, 0.64m served as the L_0 for this study. Growth rates, age of maturity and longevity were then calculated from the two parameter von Bertalanffy growth model produced from the growth parameters derived from this study.

3.5 Justification of the model

All encounter data were used to determine how the model fit for sharks encountered 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. Once every encounter had an adjusted size, each shark was given an initial age utilizing the two parameter von Bertalanffy equation determined in this 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 this 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:

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

where k is the growth parameter, L_∞ is the max size (m), L_0 is birth size (m) and L_t/L_∞ is equal to 0.95 (Hsu et al, 2014).*3.7*

Age of Maturity

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

4. Results

4.1 Regression Analysis

4.1.1 Visual and Laser Regression

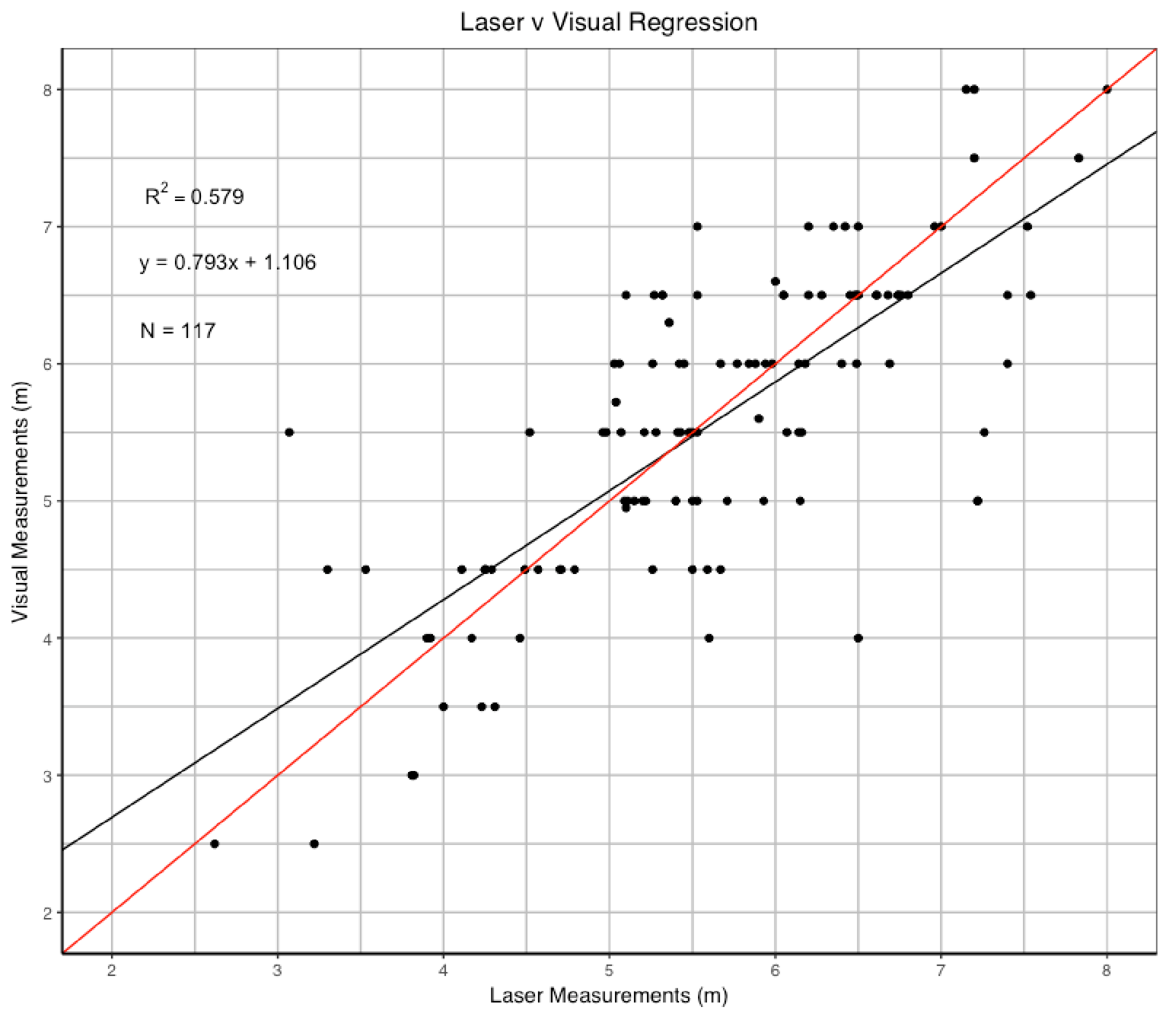

Figure 10: Relation between visual and laser measurement methods. A red line with a slope of one (perfect match) was added for visual reference

There were a total of 117 encounters where visual and laser estimates were both recorded. The results show that visual estimates tended to overestimate the total lengths of 2m to 5.4m sharks while underestimating the sizes of 5.4m to 8m sharks. The mean of visual estimates is 5.548 and the mean of laser estimates is 5.598. A regression line was produced with the following formula:

Visual Measurements = 0.7939*(Laser Measurements) + 1.1060 (R^2 =0.579).

4.1.2 Tape and Visual Regression

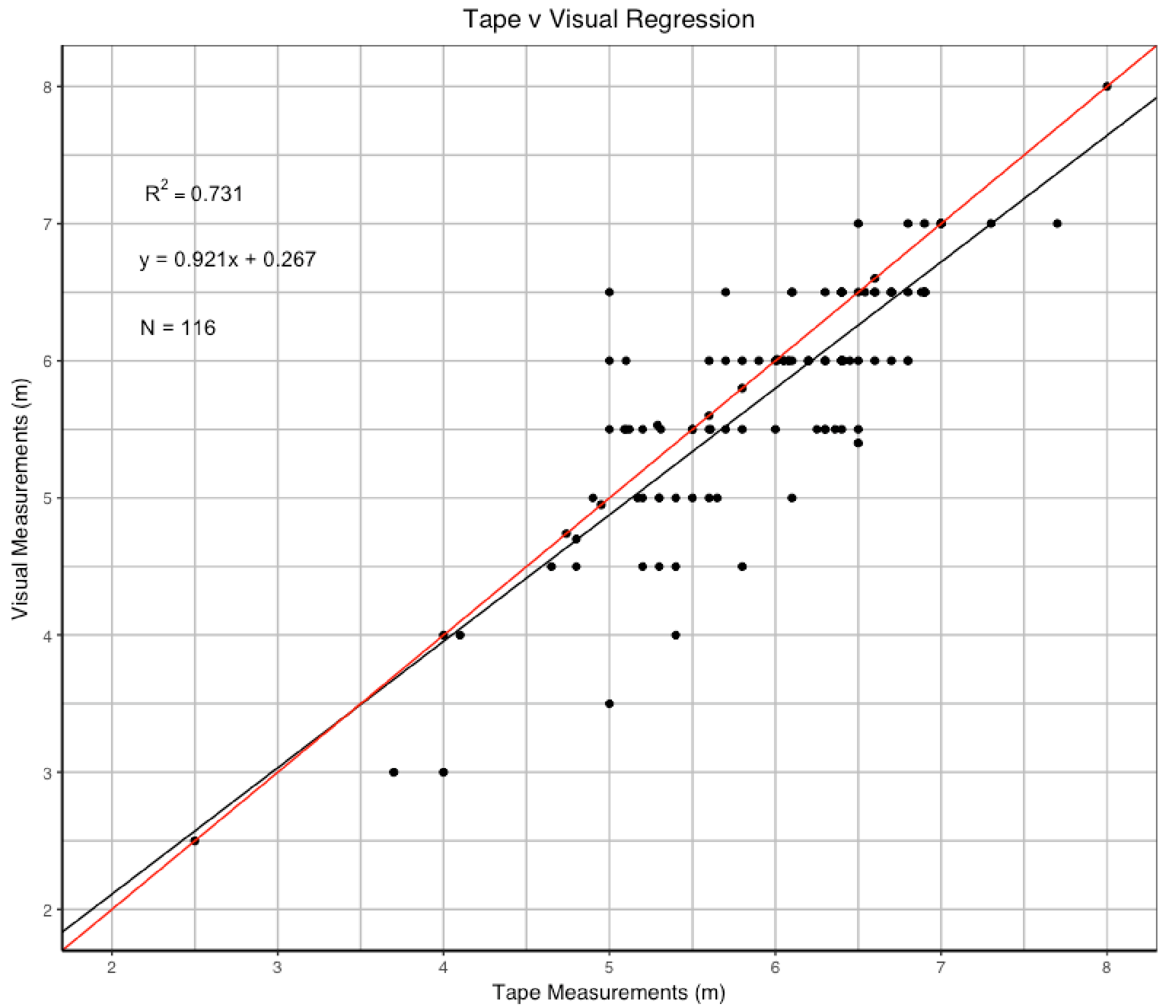

Figure 11: Relation between tape and visual measurement methods A red line with a slope of one (perfect match) was added for visual reference

There were a total of 116 encounters where tape and visual estimates were both recorded. The results show that visual estimates are good at predicting the total length of sharks between the sizes of 2m to 4m. However, visual estimates tend to slightly overestimate the size of sharks larger than 4m. The mean of visual estimates is 5.753m and the mean of tape estimates is 5.960m. The regression line formula is:

Visual Measurements = 0.9218*(Tape Measurements) + 0.2672 (R^2 = 0.731).

4.1.3 Tape and Laser Regression

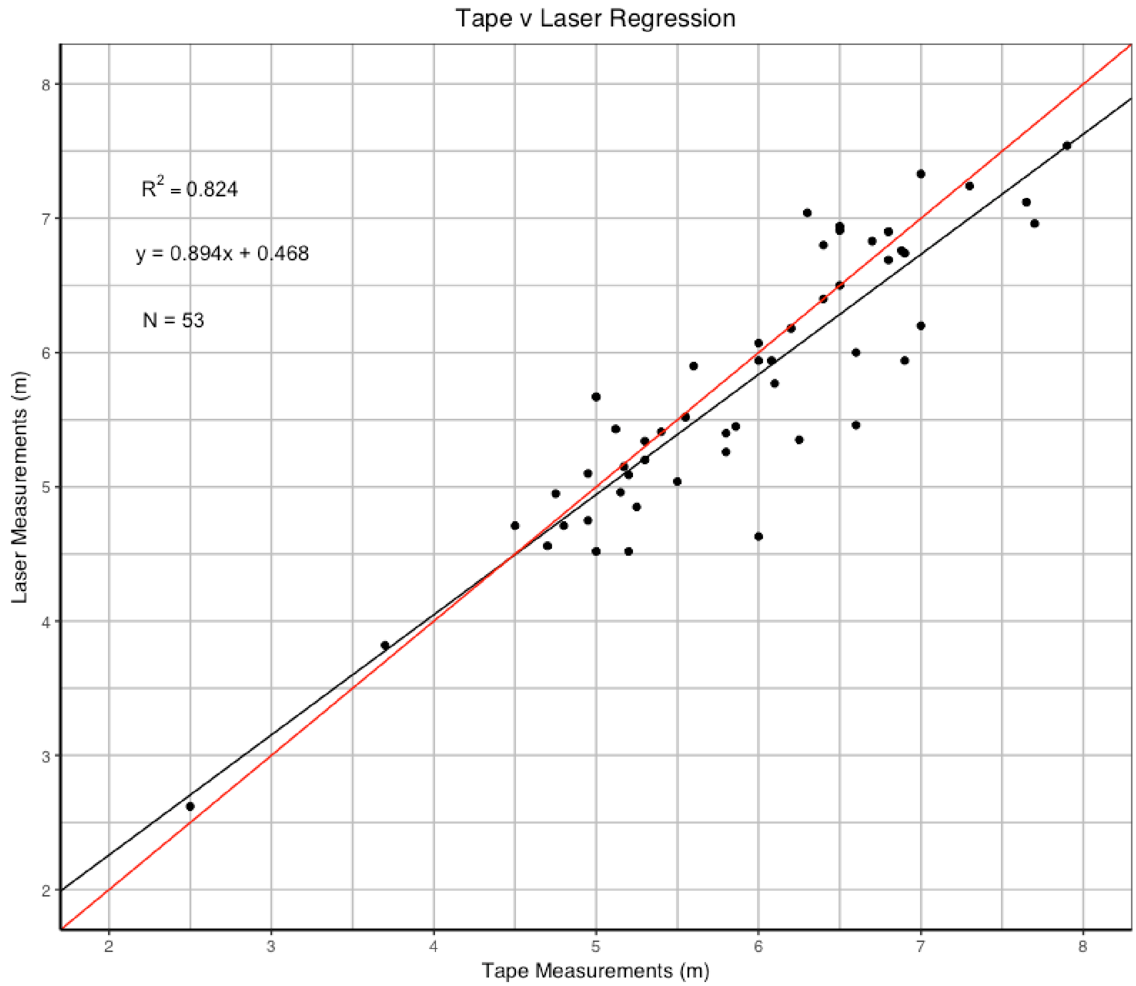

Figure 12: Relation between laser and tape measurement methods A red line with a slope of one (perfect match) was added for visual reference

There were a total of 53 encounters in which tape and laser estimates were recorded. The results show that laser estimates tended to overestimate the total lengths of sharks from 2m to 4.5m in size. They also tended to slightly underestimate sharks larger than 4.5m. The mean of tape estimates is 5.904m and the mean of laser estimates is 5.752m. The equation of the regression line is:

Laser Measurement = 0.8949*(Tape Measurement) + 0.4680 (R^2 = 0.824).

4.2 Precision of Tape and Laser Measurements

Standard deviations were calculated to determine the precision of tape and laser measurements. There were a total of 32 encounters in which 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 0.1713m. Therefore, repeated measurements utilizing the tape method may differ by ±0.1713m. There were a total of 29 encounters with 98 individual measurements in which multiple laser measurements were analyzed. The standard deviation associated with laser measurements was found to be 0.1403m. Therefore, repeated measurements utilizing the laser method may differ by ±0.1403m.

4.*3 Average Sizes of New, Transient and Returning Sharks*

A total of 942 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 13). 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 13). It is possible that if there were more days on the water then this high value would have decreased and be more in line with the other 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 labelled 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 only label produced statistically significant differences in sizes. A post hoc test showed that there was only a significant difference between new and returning sharks (Table 3).

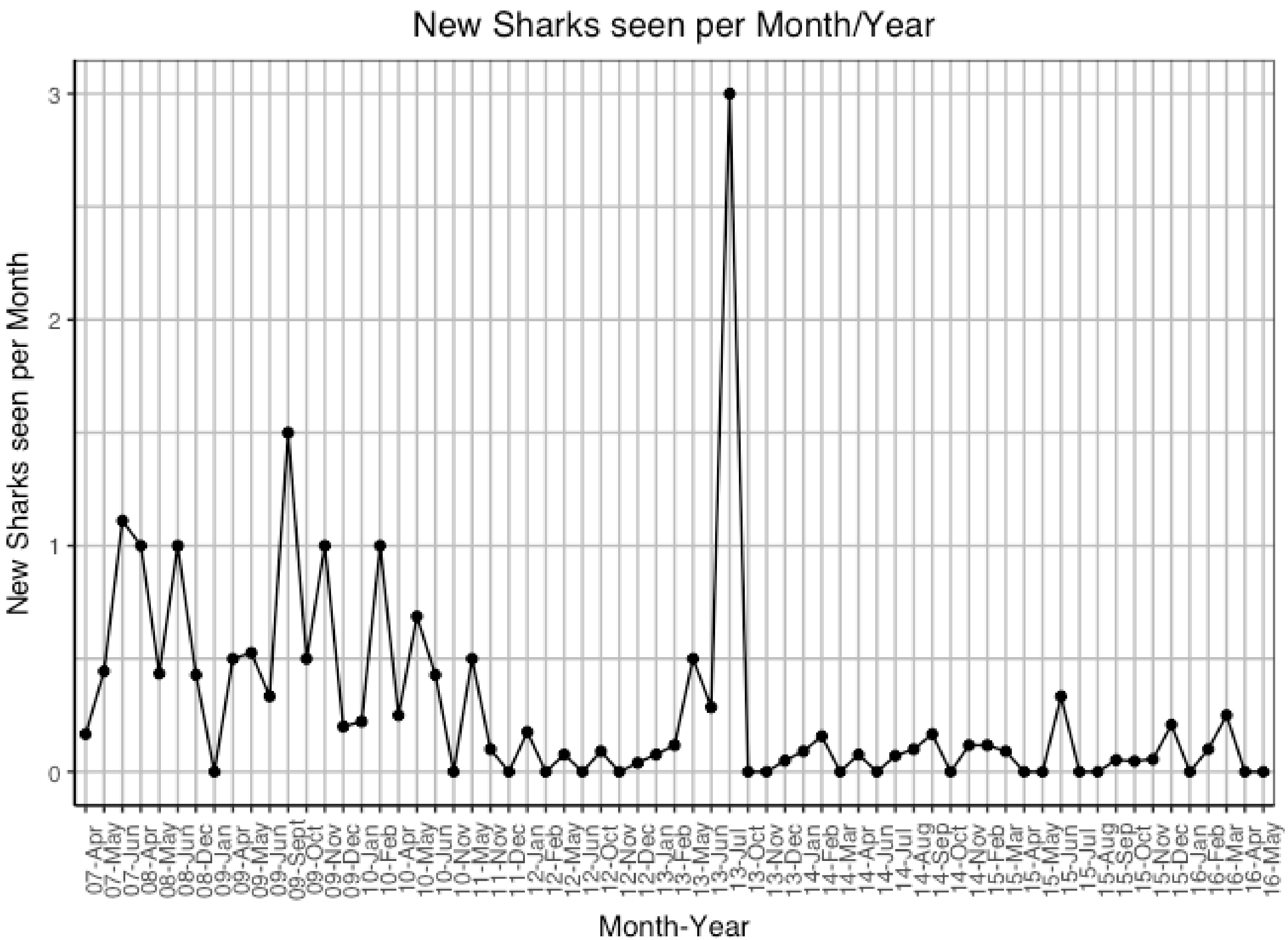

Figure 13: Average number of new sharks seen per search effort (days) throughout each month and year of study

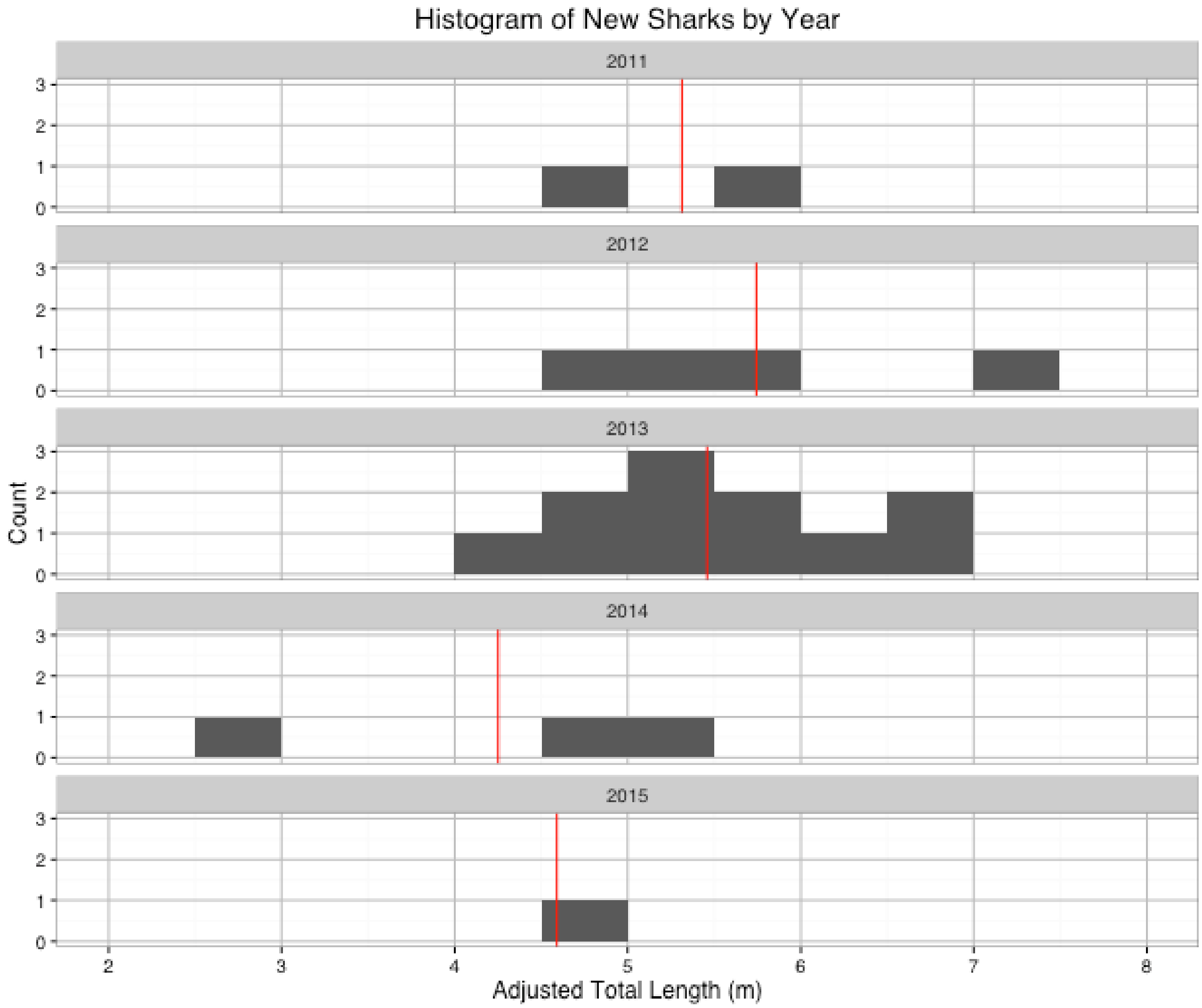

Figure 14: Size frequency of new sharks seen per year. The red line associated with each year is the average size of new sharks seen during that year

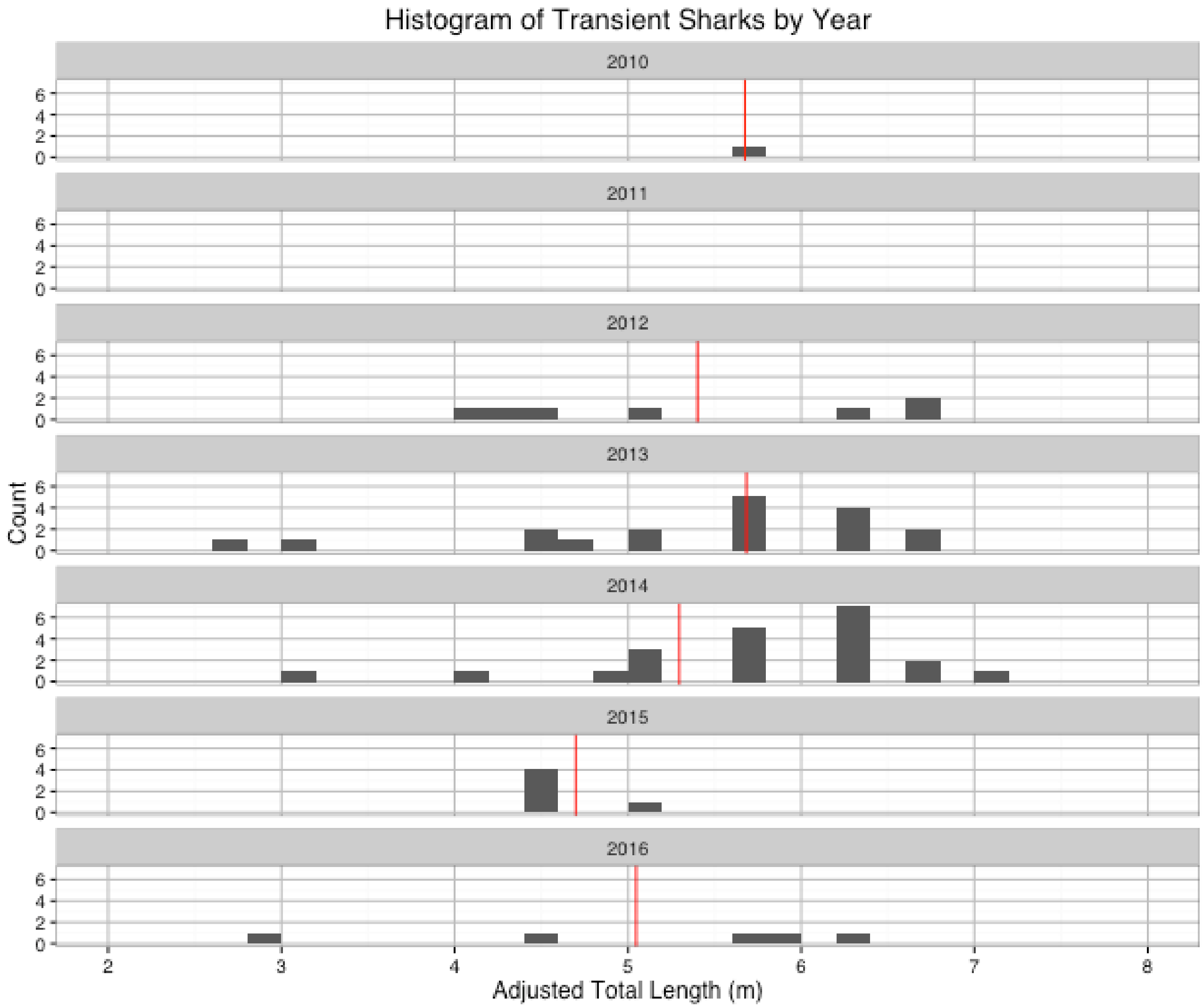

Figure 15: Size frequency of transient sharks seen per year. The red line associated with each year is the average size of transient sharks seen during that year

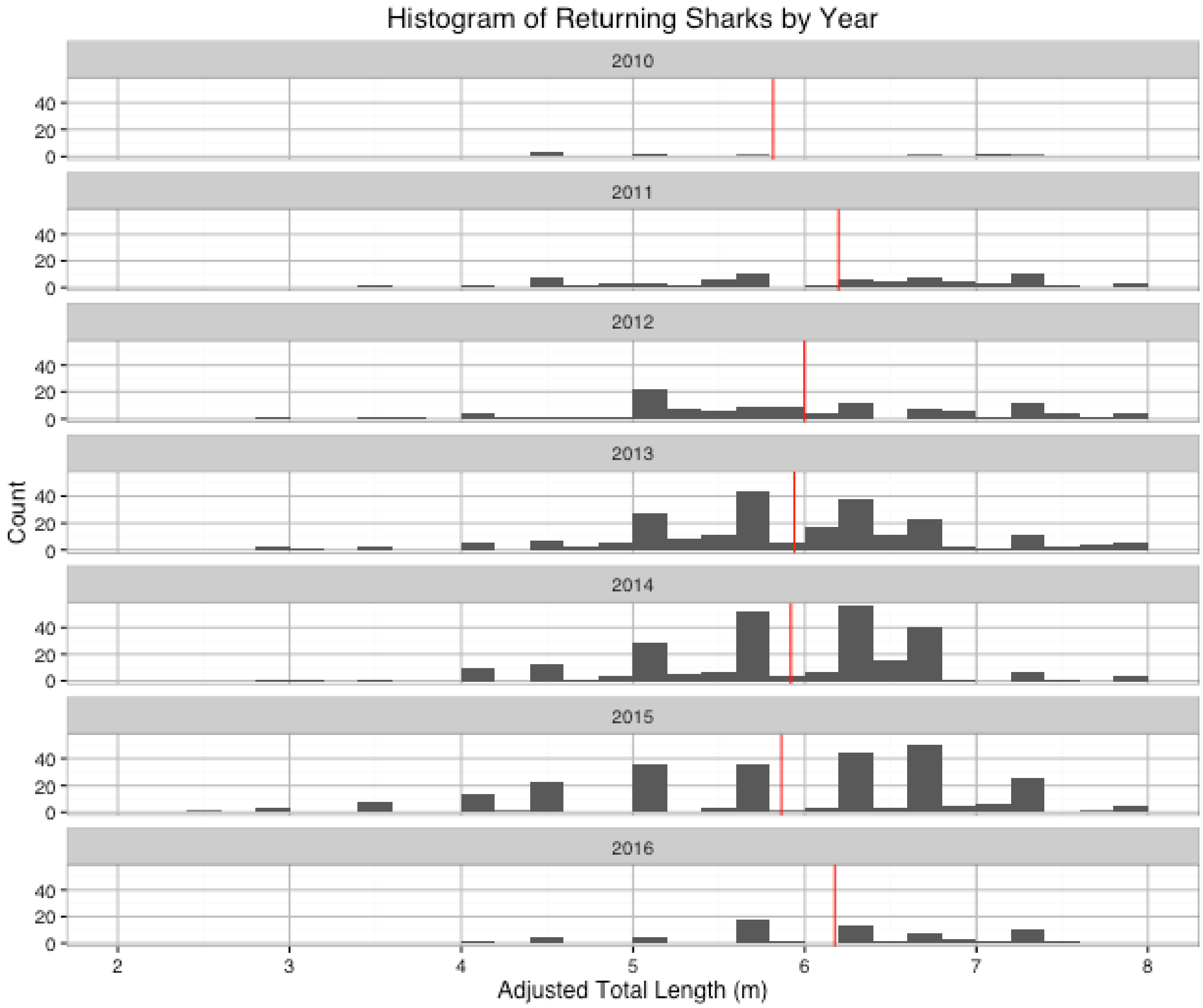

Figure 16: Size frequency of returning sharks seen per year. The red line associated with each year is the average size of returning sharks seen during that year

Table 1: Summary of average sizes by label per year

Year	*New*	*Returning*	*Transient*
2010	--	5.817	--
2011	5.313	6.197	5.676
2012	5.743	5.997	5.401
2013	5.458	5.938	5.683
2014	4.251	5.919	5.295
2015	4.591	5.865	4.699
2016	--	6.175	5.047

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 that were at liberty for at least a year. There were 177 encounters with forty male sharks and only nine encounters with four female sharks were recorded. Growth parameters were calculated for both sexes and then for males separately. Female sharks were not analyzed due to the small sample size. Six encounters that were outside of two standard deviations from the standard residuals were removed from the dataset. Solving the equation gave an L_∞ of 19.556m and a k value of $0.0211 yr^{-1}$. Only analyzing data from male sharks changed the parameters to an L_∞ of 18.081m and a k value of $0.0234 yr^{-1}$.

4.5 Age and Length

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

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

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).

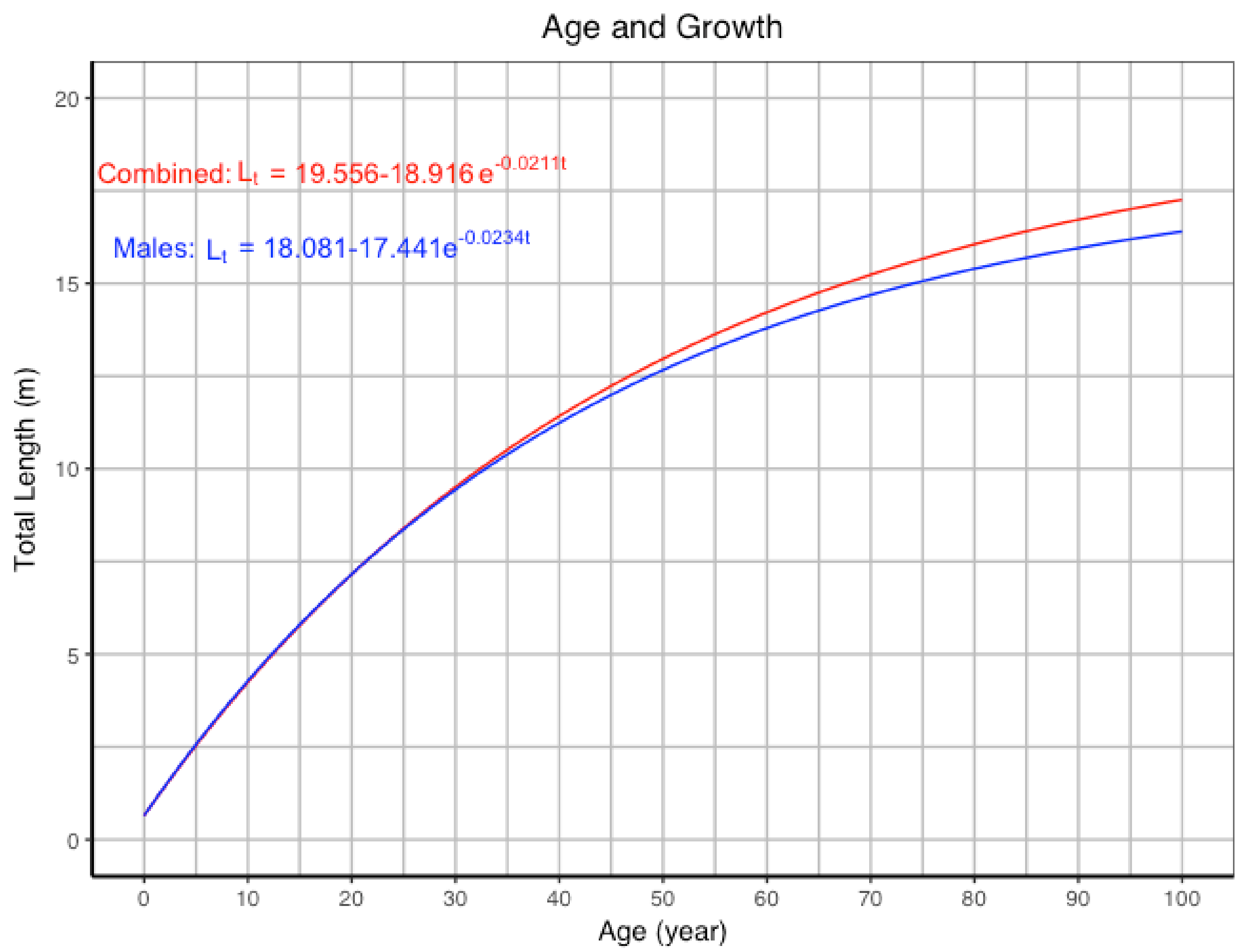

Figure 17: Age and length data from the two parameter von Bertalanffy growth equation utilizing the growth parameters derived from the nonlinear regressions

4.6 Growth Rates

Using the two parameter von Bertalanffy growth equation provides total length based upon ages and therefore can allow for the calculation of 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 sex 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 Sex*	
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. There were 1402 encounters with 106 male sharks that had measurement data recorded. The maximum and minimum age determined from the data was 26.4 and 5.5 years, respectively. The mean age of all male sharks encountered was 14.8 years. The maximum and minimum size was 8.9m and 1.88m, respectively. The mean size from all encounter data was 5.77m. Histograms of total length and age were produced in order to provide a thorough understanding of the population demographics of male whale sharks seen near the South Ari Atoll, Maldives (Figure 19 and 20).

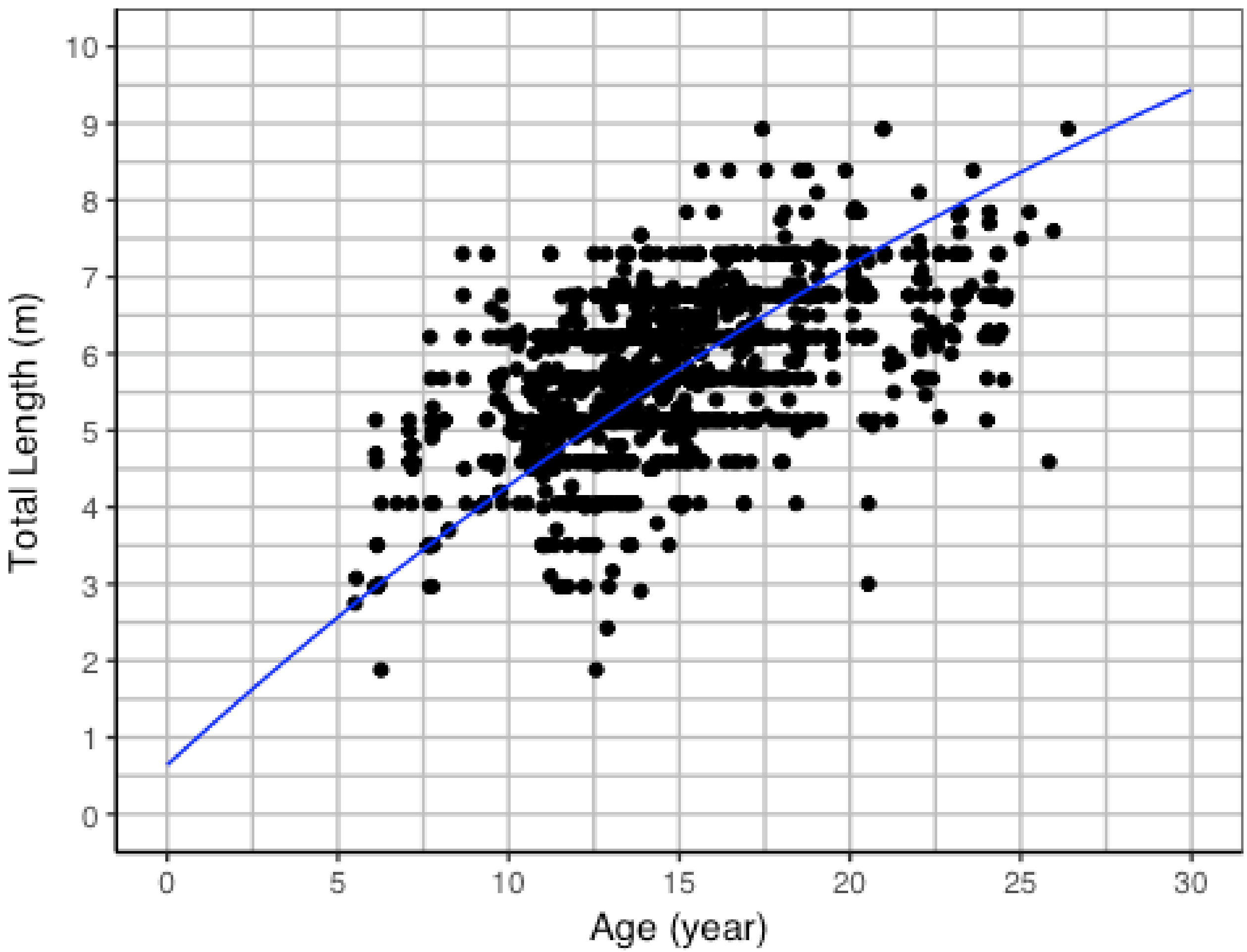

Figure 18: Age and length data for every male encounter from April 21, 2006 to May 5, 2016. The blue curve is the male two parameter von Bertalanffy growth equation determined by the nonlinear model

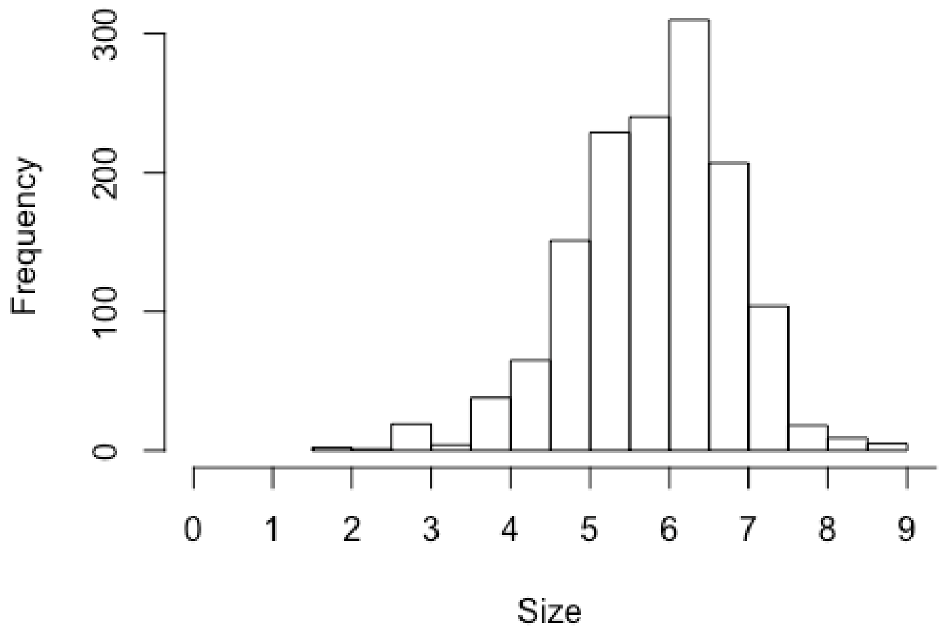

Figure 19: Histogram of total lengths of sharks encountered

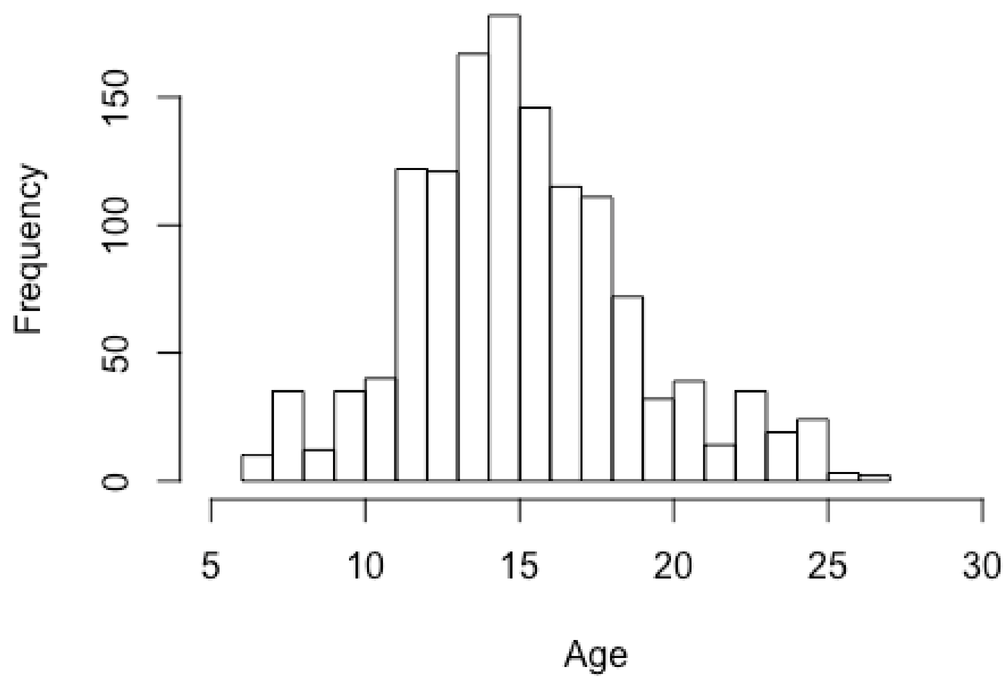

Figure 20: Histogram of ages of sharks encountered

4.8 Age of Maturity and Longevity

Assuming (male) whale sharks become mature between 8.1m and 9.1m (Eckert and Stewart, 2001), the male growth model estimates the age of maturity to be reached between 23.85 and 28.36 years, respectively. There were few sharks in this study that were in this size range, however, none were documented as mature individuals, i.e. calcified claspers. The Taylor method yielded a longevity of 135.14 years from the L_∞ of 18.081m derived from the male sharks in this study.

5. Discussion

This study was successfully able to analyze a long-term dataset and convert total length measurements to a standardized unit in order to investigate growth parameters and rates of free-swimming whale sharks in the Maldives. This allowed for the different measurement methods to be compared to one another and from this investigation biases associated with different shark sizes were studied. Once all total lengths were converted into a standardized measure then more complex analysis could occur. This allowed for the average sizes of new, transient and returning sharks to be investigated as well as growth parameters to be produced. This study represents the first growth parameters and growth rates produced from a wild aggregation of free-swimming whale sharks.

Conclusion of comparison of methods

Errors associated with visual estimates were found to overestimate small sharks and underestimate larger sharks when compared to laser measurements. 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 tape measurements. This tendency of visual estimates to underestimate larger sharks was also supported by Sequeira *et al.* (2016). This finding has implications for understanding the demographics of whale sharks worldwide, as aggregation sites utilizing visual estimates would tend to underestimate the number of mature sharks. The results from the linear regression of the different measurement methods used in the Maldives follows the pattern Sequeira *et al.* (2016) found. Visual estimates underestimated large sharks when compared to both tape and laser measurements and started to underestimate total length of sharks around 4 and 6 meters when compared to tape and laser measurements, respectively.

Tape measurements provide a much more accurate way to measure whale sharks in areas where laser equipment may be unreliable, unaffordable or impractical. The results from this study show that tape measurements are not that different from laser measurements with an R^2 value of 0.824. However, tape measurements were a much better fit for visual estimates than laser measurements, with a R^2 of 0.7315 and 0.5792, respectively. Tape measurements were much better at bridging the gap and error between visual and laser measurements. The precision associated with tape measurements was similar to the precision associated with laser measurements with standard deviation being 0.1713 and 0.1403, respectively. The accuracy of each measurement method is very difficult to interpret as the actual total length is required in order to calculate this value. These lengths are often taken from dead specimen, whereas this study used non-invasive sampling to collect data on free-swimming whale sharks. Laser measurements are thought to be more accurate and precise when compared to visual measurements (Rohner *et al.*, 2015). There was much more variability between visual and laser measurements than visual and tape measurements.

Average Sizes of New, Transient and Returning Sharks

Small sharks are likely recruited to the South Ari Atoll where they stay and grow until they reach a certain size, possibly maturity (Pers. comm. R. Rees) because new sharks were found to be significantly smaller than returning sharks. Once large, or mature, they are likely fit enough to survive the patchy open ocean environment and adopt a more pelagic lifestyle. This has important management implications as the Maldives may be a place where juvenile whale sharks grow and mature before they leave the surrounding waters. It also raises the questions of where these sharks are born before they make their way to the Maldives. However, protecting these juvenile sharks is vital for the long-term survival of the species. Transient sharks were not significantly different in size from new and returning sharks and were often smaller than returning sharks and larger than new sharks. Perhaps these transient sharks would fit into one of the other labels 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 to these atolls and/or pass the South Ari atoll on their travel between atolls (Pers. comm. R. Rees).

Growth parameters and rates

This is the first study to calculate growth parameters and rates 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 of short (1-3 year) periods. The largest change in time from this study was 7 years with a mean of 3.16 years between encounters. Only 23 of the encounters yielded a negative growth rate. When visual estimates were included in analysis it resulted in a very large L_∞ and had large chi square values. Visual measurements 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.

The combined sex von Bertalanffy parameters determined in this study are an L_∞ of 19.55m and a k value of 0.021yr^{-1}. These values differ from biannual vertebral analysis of whale sharks from the Northwest Pacific which yielded an L_∞ of 16.8m and a k value of 0.037yr^{-1} when both sexes were combined utilizing a two parameter von Bertalanffy growth function (Hsu *et al.*, 2014). However, the parameters derived in this study are more in line with the biannual parameters defined by Hsu *et al.* (2014) when male ($L_\infty = 19.7m, k = 0.03\ yr^{-1}$) and female sharks ($L_\infty = 20.5m, k = 0.029yr^{-1}$) were analyzed using a two parameter von Bertalanffy growth equation separately. The L_∞ and k values for combined sex of this study are also almost identical to Wintner's (2000) study where one of the von Bertalanffy growth curves yielded a L_∞ of 19.66m and a k value of 0.021yr^{-1}. Pauly (1997) estimated tentative values of L_∞ of 14m and a k value of 0.03yr^{-1} (Bradshaw *et al.*, 2007). All whale shark growth parameters have been summarized in Table 7. The corresponding total length and growth rate related to ages is summarized in Table 8 and 9.

The male only growth parameters derived from this study (L_∞ =18.08m, k = 0.023) are slightly lower than the biannual male only growth parameters determined by Hsu *et al.* (2014). However, Hsu *et al.* (2014) could not rule out annual band pair formation when they were investigating vertebrae. Male growth parameters derived from annual band formation (L_∞=18.023m, k=0.017yr^{-1}) determined by Hsu *et al.* (2014) were similar to the L_∞ of 18.08m and k value of 0.023yr^{-1} determined by male sharks in this study.

The L_∞ of 18.081m and 19.556m determined in this study fit in line with the largest sharks documented in the literature. Compagno (2001) claimed an L_∞ of 21.4m and Chen *et al.* (1997) observed a specimen from a Taiwan fish market that appeared to be around 20m. However, the second largest whale sharks are near 18m and the largest scientifically measured whale shark was an 18.8m female shark (Borrell *et al.*, 2011; McClain *et al.*, 2015). The 18m shark identified by Eckert and Stewart (2001) was also female. Therefore, the combined sex L_∞ of 19.55 derived in this study fits in the range of the largest whale sharks documented at 18m – 20m and is similar to the largest scientifically recorded female whale shark of 18.8m (Table 5).

This study determined a k value of 0.02yr^{-1} for both combined and male sex. The growth coefficient k describes the rate at which an individual reaches maximum size from its size at birth. 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 in which energy is used primarily for movement more than growth (Hsu *et al.*, 2014).

This study documented a growth rate that began at ~40 cm yr^{-1} after birth and declined to ~26 cm yr^{-1} by age 20. The large range of growth rates in wild free-swimming whale sharks is likely a result of large margins of errors 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 differ between sexes, size classes and geographic location. This study consisted of a majority of juvenile male whale sharks. Females may exhibit separate growth rates and small individuals may grow much faster than the size class in this study. There is a paucity of information of small whale sharks and only 19 sharks <1.5m 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 this study.

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

Total Length (m)	References
18.8	North-western 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)
19.55	**This Study (Combined Sexes)**
18.08	**This 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 0.64m

$L_\infty(m)$	k (yr^{-1})	t_{max} (years)	Method	Location
19.556	**0.0211**	**142.5**	**Free-swimming (N=44)**	**South Ari Atoll, Maldives (Combined Sexes)**
18.081	**0.0234**	**135.14**	**Free-Swimming (N=40)**	**South Ari, Atoll, Maldives (Males)**
16.8	0.037	89.53	Vertebrae (biannual) (Combined Sex N=95)	Northwest Pacific (Hsu *et al.*, 2014)
19.7	0.03	99.74	Vertebrae (biannual) Males (N=44)	Northwest Pacific (Hsu *et al.*, 2014)
20.5	0.029	103.91	Vertebrae (biannual) Females (N=31)	Northwest Pacific (Hsu *et al.*, 2014)
15.34	0.021	166.84	Vertebrae (annual) (Combined Sex N=95)	Northwest Pacific (Hsu *et al.*, 2014)
14.96	0.032	111.19 (extrapolated)	Vertebrae (Combined Sex N=15)	South Africa (Wintner 2000)
19.66	0.021	142.69 (extrapolated)	Vertebrae (Combined Sex 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 are UK for unknown, M for males and 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**	**19.55**	**39.5**	**This study**
M	**Wild**	**Tape and Laser**	**0.64**	**18.08**	**40.3**	**This 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 sex growth parameters derived from vertebral analysis by each study to determine age and growth

	Combined Sex					
	This 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 sex growth equations derived from vertebral analysis by each study to determine age and growth

	Combined Sex					
	This 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 this study and biannual and annual band formation derived from Hsu *et al.* (2014)

	Males		
	This Study	Hsu *et al.* (2014) Biannual	Hsu *et al.* (2014) Annual
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

Age of Maturity and Longevity

A male age of maturity ~25 years and a longevity of ~140 years determined by this 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 an extrapolated longevity from one of Wintner's (2000) von Bertalanffy growth equations yielded a similar longevity of ~140 years to this study (Table 6).

6. Conclusion

This 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 underrepresented in the literature. There may actually be larger sharks appearing at aggregation sites worldwide than previously thought. While none of the sharks in the South Ari Atoll, Maldives are mature, this may change the population demographics at other aggregation sites that utilize only visual estimates to determine total lengths.

The significant differences between the label of sharks throughout the years of the study has some support to the theory that small juvenile whale sharks are arriving to the Maldives and staying throughout the years until they reach a certain size or maturity. The largest sharks in this study were 8.9m and immature but within the range of documented size at maturity. No sharks larger than 8.9m 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 to stay and grow but not suitable for larger mature individuals.

The growth rates determined in this 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. Sixty-nine percent of the sharks seen in the South Ari MPA have some sort of documented injury. Seventy-eight percent of these injuries were classified as anthropogenic. These injuries may have an effect on the growth rates of whale sharks as resources and energy will likely be contributed to the healing of the injury and not necessarily the growth of the animal. This may slow the growth of whale sharks in the Maldives and affect the L_{∞} and k values that were generated in this study. Speed *et al.* (2008) found similar percentages of injuries at other aggregation sites in the Indian Ocean. There also may be differences in growth rates of whale sharks by sexes. 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). There were only 9 encounters with 4 female sharks and therefore sex specific growth rates were not determined. Growth rates in wild populations have shown larger ranges and are likely the result of errors in measurement methods. Utilizing more accurate measurement methods (tape and laser) in this study allowed for a more accurate representation of growth rates in the wild. An L_{∞} of 19.556 and a k value of 0.0211yr^{-1} for both sexes are consistent with the literature and are the first growth parameters defined from an aggregation of free swimming whale sharks. These correlate to a longevity of over 140 years. Utilizing male growth parameters yielded a sexual maturity of ~25 years for male sharks in the Indo-Pacific.

The results of this study have important implications into 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 the population. It is also important to note that these parameters might change at different geographic locations and between the sexes. Similarly, 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). Long life spans (140 yrs.) and slow growth ($k=0.02yr^{-1}$) mean that the impact of whale shark fisheries may still be experienced worldwide. Anecdotal conversations with experienced whale shark fishermen indicated that total lengths of the sharks they used to catch were much larger than the sizes of sharks seen today in the Maldives. They also reported greater number of whale sharks and numerous encounters with more than one shark at a time which is infrequent within this aggregation site (personal communication). 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.

One of the greatest challenges to conservation of whale sharks is the poor understanding of important life-history characteristics (Pravin, 2000). A more thorough understanding of age and growth parameters will lead to better estimates of the ability for populations to be able to grow and recover from overexploitation. Furthermore, a better understanding of age of maturity and longevity is vital for effective management plans (Goldman *et al.*, 2012). This study aims to add to information on age and growth from wild populations of whale sharks and is the first study to develop growth parameters from free-swimming whale sharks. Providing precise and accurate life-history parameters is necessary in order to determine population status. It is important to note that growth rates, age and growth, size at maturity and longevity may differ by sex and geographic location. A better understanding of whale shark demographics at other aggregation sites will provide important answers into these questions. The use of more accurate measurement techniques at aggregation sites worldwide is needed 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:	Date:	Time Start Searching:	Time Stop Searching:	Breaks (Hrs):	Encounter Number: ________of________

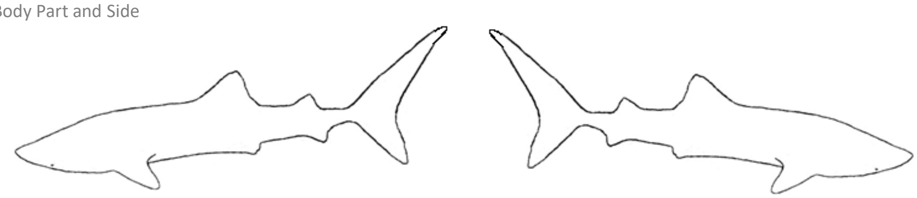
Time Encounter:	Encounter Duration:	Location:	Coordinates North:	Coordinates East:

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