

**Environment Department**

**University of York**

**Assessment Submission Cover Sheet 2016/17**

***This cover sheet should be the first page of your assessment.***

<b>Exam Number:</b> Y3845466 <i>Examination Number (this number will start with a 'Y' – it is available on the back of your student ID card)</i>	<b>Module Code:</b> ENV00068M
<b>Module Title:</b> Dissertation	<b>Assessment Deadline:</b> 3.7.2017

I confirm that I have

- conformed with University regulations on academic integrity
- Please insert word count
- not written my name anywhere in the assessment
- checked that I am submitting the correct and final version of my coursework
- saved my assessment in the correct format
- formatted my assessment in line with departmental guidelines
  - I have ensured my work is compatible with black and white printing
  - I have ensured the compatibility of any graphs or charts included in my submission
  - I have used 12pt font (preferably Arial or similar)
  - I have ensured all pages are clearly numbered using the system 1 of 6, 2 of 6 etc. Page 1 will be your Assessment Submission Cover Sheet
  - I have ensured my examination number is on every page of the assessment

**PLEASE TICK BOX TO CONFIRM**

**Please note: if you have any questions please see the FAQs on the VLE**



UNIVERSITY  
*of York*

**Characteristics of whale shark *Rhincodon typus* around the island of St Helena, South Atlantic & the comparative impact of ecotourism**

Katie Hindle

Y3845466

MSc Marine Environmental Management

2017

Word Count: 4975

Supervisor: Callum Roberts

## **Disclaimer**

I declare that the work and analysis reported in this dissertation is my own, except where stated (in acknowledgements). I declare this work to be 4975 words, excluding title page, report title, acknowledgements, figures and legends, reference list and this disclaimer.

Signature K. Hindle

Date 28.06.2017

## **Acknowledgements**

Thank you to Maldives Whale Shark Research Programme for the time I worked with them collecting data and their help with providing me with the most recent reports. Thank you to Marine Conservation Section of St Helena Government and to Al Dove, Rafael de la Parra and the research team from Georgia Aquarium for allowing me to join them on their boat to work with them collecting data. Thank you to Jason Holmberg for providing access to the online database wild book for whale sharks. Thank you to Callum Roberts for help and advice and to friends and family, especially Morgan Riley, who provided support and encouragement throughout the project.

## Abstract

328 whale sharks (*Rhincodon typus*) were identified using photographs and pattern recognition software between 2013 and 2017 around the island of St Helena in the South Atlantic. The highest number of whale sharks were recorded in the month of January. This is probably due to the sharks exploiting a seasonally abundant food source, such as tuna (*Scombridae* spp.) and other fish spawn in the waters around St Helena. Other behaviours observed included females remaining stationary in an inverted arc posture with males swimming around them, which is associated with mating behaviour in other shark species. The mean total length of the sharks was 7.63 metres, and of the sharks whose sex was determined 45.9% (133) were female, and 54.1% (157) male. Of those males, only one was juvenile as determined by clasper morphology. Worldwide, aggregations of whale sharks tend to consist of majority juvenile males. The combination of mature male and female whale sharks in the study area and the observed courtship behaviour means it is possible that the waters around St Helena are of global importance for whale shark mating.

The St Helena aggregation was compared to an aggregation in the Maldives with 315 whale sharks identified over 10 years. Whale sharks in the Maldives bore a significantly higher injury rate (82.2%,  $p < 0.001$ ,  $X^2$  test) than those in the St Helena aggregation (9.1%), with anthropogenic injuries in Maldives at 54.9%, compared to 2.4% in St Helena. This may be a consequence of the greater number of weakly regulated ecotourism boats targeting the Maldives aggregation compared to the tightly regulated and limited ecotourism for whale sharks around St Helena.

## Introduction

The whale shark *Rhincodon typus* was first described in 1828 by physician Andrew Smith from a specimen harpooned in Table Bay, South Africa (Smith, 1828). *R. typus* are Orectolobiformes, part of the carpet shark family, with morphological and anatomical features including two dorsal fins; a transverse mouth that does not extend behind the eyes;

and, barbels beside the nostrils (Colman, 1997; Compagno, 1984). Whale sharks have five gill slits and a spiracle which is used in respiration (Compagno, 1984); a large primary dorsal fin; and, three longitudinal dermal ridges (Rowat & Brooks, 2012; Colman, 1997; Taylor 2007). One of three known filter feeding elasmobranch species along with the basking shark (*Cetorhinus maximus*) and megamouth shark (*Megachasma pelagios*), whale sharks are the largest known fish. A specimen with a measured total length of 12.18 m (Karbhari & Josekutty, 1986) is the largest recorded, however whale sharks exceeding 18 m have been reported.

The longitudinal dermal ridges contain Ampullae of Lorenzini that detect electromagnetic fields and changes in water pressure (Rowat & Brooks, 2012; Colman, 1997; Taylor 2007). Whale shark inner ears are the largest in the animal kingdom suggesting their hearing is very good, particularly at detecting very low frequencies (Myrberg, 2001). Although their eyes are small, they are sensitive to low light environments and can pick out objects and see movement at close range (between 3 and 5 m) (Martin, 2007). In general Chondrichthyes' sense of smell is extremely sensitive, using chemo sensory detection through the olfactory capsules (Hueter et al 2004), but the role of this in whale sharks is largely unknown (Rowat & Brooks, 2012; Klimley, 2013).

Whale sharks have many rows of tiny teeth but feed by filtering large volumes of water along with prey through their gill rakers. They are known to feed on plankton (Nelson & Eckert, 2007), krill (Wilson et al, 2001; Taylor, 2007), fish spawn (de la Parra Venegas et al, 2011) and small schooling fish (Duffy, 2002). Recent tagging studies have shown whale sharks are able to dive to depths beyond the pressure tolerance of the tags (3500 m) (Thums et al, 2012) where temperatures of as low as 2.2°C (Rowat & Brooks, 2012).

Whale shark sex can be determined by the presence or absence of claspers between the pelvic fins; they are absent in females. Clasper development can be used to identify male maturity: immature males have short uncalcified claspers whilst mature males' claspers

extend beyond the pelvic fins (Holden & Raitt, 1974) and after copulation become calcified and torn (Rohner et al, 2015; Holden & Raitt, 1974). Female sharks are thought to be mature at around 8m (Hearn et al, 2016).

Whale sharks have been recorded across all warm temperate and tropical waters (Compagno 2001), though their local abundance varies greatly from place to place. Whale sharks are capable of far ranging movement; for example, an individual tagged in the Sea of Cortez swam 21,000 km over 37 months (Eckert & Stewart, 2000), but it is not known if migration takes place. Seasonal aggregations have been identified and are most prominent on the west coast of Australia, Gulf of Mexico and the Indian Ocean where the South Ari atoll in the Maldives hosts the only known year round aggregation site (Sequiera et al, 2012; Riley et al, 2010). These aggregations usually demonstrate a strong juvenile male bias and are associated with seasonally abundant food sources (Heyman et al, 2001; Wilson et al, 2001). There are only a few locations where mature females have been found and even fewer where mature males and females are found together, including the Gulf of Mexico (Ramirez-Macias et al, 2007), Galapagos (Acuna-Marrero et al, 2014) and St Helena as reported here.

Knowledge of whale shark reproduction comes almost exclusively from a single gravid female landed in Taiwan in 1995. 304 embryos of different stages of development were inside her (Joung et al, 1996). This demonstrated ovoviviparity. Very few neonates have been reported free swimming in the ocean but it is thought that pups are less than a metre long at birth (Hussey et al, 2010). There are distinct morphological differences between neonatal and adult whale sharks. Neonates have a more curved caudal fin held at a more acute angle, relatively smaller pectoral fins, and an elongated body (Wolfson & Notarbartolodi-Sciara, 1981, Kukuyev, 1996). Growth rates of whale sharks have been documented through direct measurement in aquariums and using laser photogrammetry in the wild (Rohner et al, 2011). Laser photogrammetry is commonly used by whale shark research

teams although the accuracy is reliant on the correct preparation and operation of the laser array which makes this method vulnerable to error (Webb et al, 2016).

The greatest natural threat to whale sharks is probably from predators when they are neonates: they have been found in the stomachs of other sharks and blue marlin (Colman, 1997; Kukuyev, 1995). Neonatal pups grow faster than juveniles (Chang et al, 1997) which could be an evolutionary response to reduce the risk of predation. Adult whale sharks are subject to attacks by other shark species (Rowat et al, 2007; Speed et al, 2008), orcas (*Orcinus orca*), and false killer whales (*Pseudorca crassidens*) (O'Sullivan & Mitchell, 2000). Their defensive response when encountering these predators is to protect their more vulnerable undersides by banking and rolling away from threats (Martin, 2007; Pers. Obs., Maldives, 2013). Pictures from Ningaloo reef, Western Australia, showed a whale shark completely upside down after an orca swam underneath (Jess Hadden, Pers. Comm., 2017). Other natural threats include strandings such as those off the coast of South Africa, which are thought to be due to a combination of topography, swells, and a change in water temperature which affected the sharks' metabolism (Beckley et al, 1997).

Anthropogenic threats present the greatest risk to whale sharks. The species is protected by the Convention on International Trade in Endangered Species (CITES) under Appendix II (Figure 1). Historical hunting for their liver oil has all but stopped (helped by readily available, cheap synthetic alternatives), but hunting continues for the illegal sale of meat and fins in China and Taiwan (Chen & Phipps, 2002). Whale sharks are regularly by-catch in the fishing industry (SPC-OFP, 2012) and although some are released alive, many more are killed (Amande et al, 2010; Moazzam et al, 2016). For those that become entangled in nets, swimming with parts of net and rope attached to them causes severe injuries (Pers. Obs., Maldives 2014).

Whale sharks have thick dermal layers covered with dermodenticles (Wilson & Martin, 2003), but because they often feed at the surface they are vulnerable to collisions with vessels travelling at speed which can lead to lacerations from propellers, blunt trauma and

partial-amputation of fins (Speed et al, 2008; Meekan et al, 2006; de la Parra-Venegas et al, 2016). This is recorded in increasing frequency in areas where commercial whale shark ecotourism occurs (Womersley et al, 2016). Although whale sharks can recover from serious injuries (Riley et al, 2010) it presumably reduces individual survivorship and fecundity.

Appendix II lists species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled. It also includes so-called "look-alike species", i.e. species whose specimens in trade look like those of species listed for conservation reasons (see [Article II, paragraph 2](#) of the Convention). International trade in specimens of Appendix-II species may be authorized by the granting of an export permit or re-export certificate. No import permit is necessary for these species under CITES (although a permit is needed in some countries that have taken stricter measures than CITES requires). Permits or certificates should only be granted if the relevant authorities are satisfied that certain conditions are met, above all that trade will not be detrimental to the survival of the species in the wild. (See [Article IV](#) of the Convention)

**Figure 1:** CITES Appendix II definition (<https://cites.org/eng/app/appendices.php>)

Ecotourism is becoming an ever-increasing threat with regards to changing behaviours and boat strike injuries (Trujillo-Córdova et al, 2016). Whale sharks are slow maturing species - estimated to reach sexual maturity at around 30 years old (Taylor, 1994) – which increases their vulnerability (Bradshaw et al, 2008). Due to the global movement of whale sharks between different ocean jurisdictions, conservation and protection is difficult to manage. Species protection in one habitat but not in another close by means numbers continue to fall even in protected areas. Decreasing global whale shark numbers were discussed in the 4<sup>th</sup> International Whale Shark Convention in Doha in 2016 (Norman, 2016), this led the status of whale sharks on the IUCN Red List to be moved from vulnerable to endangered (Figure 2).

Based on count data, modelled population estimates and habitat availability, 75% of the global Whale Shark population is inferred to occur in the Indo-Pacific, and 25% in the Atlantic. A variety of datasets present declines of 40-92%, inferring an overall decline of 63% in the Indo-Pacific over the last 75 years (three generations), resulting in a subpopulation assessment of Endangered A2bd+4bd. In the Atlantic, the overall population decline is considered to be lower at  $\geq 30\%$ , resulting in a subpopulation assessment of Vulnerable A2b+4b. Given the bulk of the global population occurs in the Indo-Pacific, the overall global decline is inferred to be  $\geq 50\%$ . Globally, the Whale Shark is therefore assessed as Endangered A2bd+4bd.

**Figure 2:** IUCN Red List Endangered Definition

(<http://www.iucnredlist.org/details/summary/19488/0>)

## **Aims**

Specialised research on *R. typus* only really started from 1985. With continued advances in technology and increased public interest there are now over 50 sites globally where whale sharks are known to aggregate and numerous research programmes with tags, drones and other resources helping to improve knowledge on the species (<https://www.whaleshark.org/> 2017). This paper sets out the characteristics of the little-researched St Helena whale shark aggregation. It goes on to compare this aggregation to one in the Maldives, exploring the frequency of whale shark injuries attributable to boat strikes between two sites: St Helena which has little ecotourism, and Maldives which has a well-developed and high intensity whale shark tourist industry (Cagua et al, 2014).

## **Research Sites**

St Helena is a relatively young volcanic island of 122 km<sup>2</sup> in the South Atlantic Ocean and is a British Overseas Territory. At 15°57' S latitude and 005°43' W longitude, it has a sub-tropical climate with sea surface temperatures between 15 and 28°C. There are seamounts just off the island that rise up to as shallow as 11 metres below sea level. Whale sharks have been observed here for 8 years mainly between December and April - the summer season in St Helena - when the sea surface temperature is warmer. Each season the whale sharks are usually first recorded at the seamounts, moving to the coastal waters of the island as tuna shoals gather there to spawn. St Helena has strict rules controlling whale shark tourism, with Environmental Protection Ordinance and guidelines enforced by the Marine Section of St Helena Government (St Helena Government, 2016). All marine tourism boats in the Economic Exclusion Zone (designated as a Marine Protected Area (MPA)) must be licensed to undertake these activities and have passed an accreditation scheme (St Helena Government, 2016). A maximum of 8 people are allowed in the water with a whale shark at any one time; touching the animal, flash photography and swimming in front of the shark is

prohibited; and people have to maintain a minimum distance of 3 metres from the shark. The total interaction time allowed with a shark is 45 minutes. The regulations regarding boats include one boat per shark; maximum speed of 6 knots; and, the boat must maintain a minimum distance of 100 m from the shark at all times with engines turned off at this distance. These rules are studiously obeyed (Pers. Obs., St Helena 2016).

The Maldives archipelago is located in the central part of the Indian Ocean on the Laccadive-Chagos ridge, 03°20' N latitude and 73°22' E longitude. The Maldives covers an area of approximately 107,500 km<sup>2</sup>, only 0.3% of which is land. It consists of 1192 islands over 26 atolls running north to south (Khan et al, 2010). The inner seas of these atolls are generally between 250 and 300 m deep with the lagoons inside the atolls between 30 and 80 m deep. The channels between the atolls can be over 1000 m deep. The edges of the atolls are made up of fringing reefs and thilas with high levels of biodiversity supported by the coral and fish life (Riley et al, 2010). However, the coral reefs have been affected by rising ocean temperatures, with many sites exhibiting almost complete coral bleaching (Perry & Morgan, 2017). The climate is tropical - warm and humid year round with two distinct monsoon periods, and with sea surface temperatures between 28 and 32°C. There are 32 MPAs in the Maldives with varying levels of management and enforcement. The South Ari atoll MPA was the location for the research reported here. It was designated in 2009 but has no management plan. Although there are best practice guidelines for whale shark encounters this area is not actively managed and guidelines are not enforced.

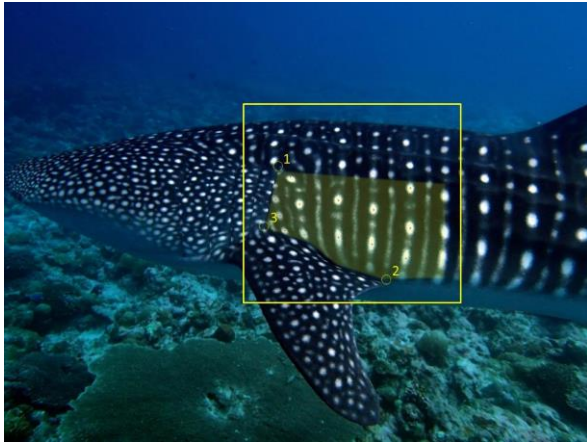
## **Field Study Methods**

Searches for *R. typus* around the island of St Helena were conducted by a dedicated whale shark research team from Georgia Aquarium in Atlanta who visited the island for a total of 12 days in 2016 and 12 days in 2015. The research team search hours on the water were between 0900 and 1600 UTC daily. Opportunistic sightings continued outside of the research team's dedicated time by means of whale shark tourist trips, *ad hoc* sightings by fishing boats, dive trips and visiting vessels. If a whale shark was sighted the encounter was

reported to the Marine Conservation Section of the St Helena Government who recorded all data on Wildbook for Whale Sharks ([www.whaleshark.org](http://www.whaleshark.org)) – an online platform visual database for people to upload their ID photos of whale sharks, the Wildbook team then processed the pictures and searched for a match online. Searches in the Maldives were conducted by a dedicated research team who spent 5 days out of 7 on the water searching for sharks each week (except during Ramadan). Typical search periods were also from 0900 to 1600 UTC daily. All data were recorded by the research team who directly used the I3S software (Interactive Individual Identification System, <http://www.reijns.com/i3s/>) to assist with photographic identification as described below.

At both sites, when a whale shark was spotted the boat was manoeuvred alongside the animal and dropped swimmers with snorkels into the water to observe behaviour, sex, record total length and take photos of injuries and the shark's spot pattern. Another researcher recorded data on the boat. Data collected included number of people in the water with the shark, number of vessels in the vicinity, location, behaviour of shark and environmental parameters.

Whale sharks have unique body pigmentation pattern of spots and stripes that remain relatively stable over time so can be used to identify individual sharks (Arzoumanian et al, 2005; Tienhoven et al, 2007). By taking photographs of specific area on both sides of the shark within set boundaries – behind the gills, before the first dorsal fin and above the pectoral fin (Figure 3) individuals can be compared using pattern recognition software. The algorithms can determine a match among pictures of whale sharks already in the database. If a match isn't found a new unique shark identification number is assigned.

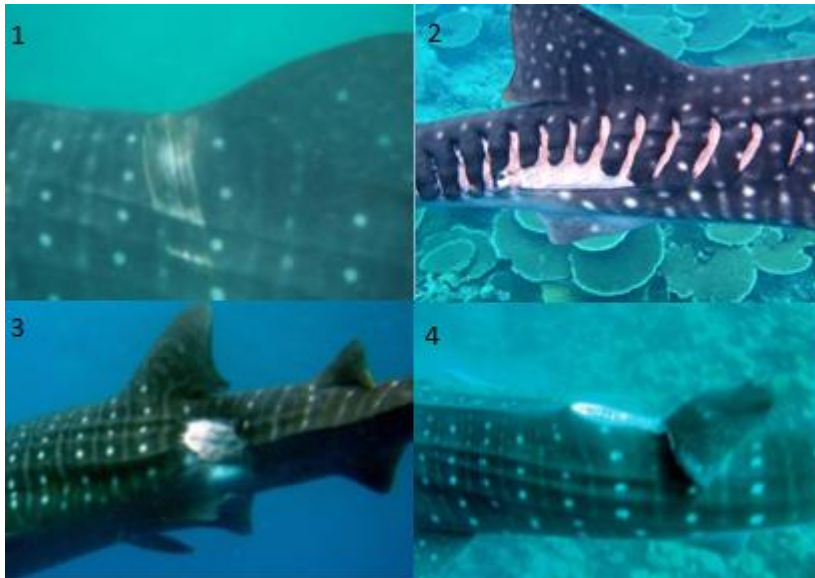


**Figure 3.** Area used for photographic identification. 1) behind the gills, 2) before the first dorsal fin and 3), above the pectoral fin.

Whale shark behaviour were classified in four main categories – *evasive*, *positive behaviour change*, *cruising*, and *feeding*. *Evasive* behaviour equates to the shark immediately moving away from the observers (Quiros, 2007). *Positive behaviour change* was determined when the shark changed direction to approach observers or the boat. *Cruising* described the shark swimming in a consistent direction not engaging in feeding behaviour (Nelsen & Eckhert, 2007). Feeding behaviour was divided in to three categories: *active ram filter feeding*; *passive ram filter feeding*; and *suction feeding* (Motta et al, 2009). *Active ram filter feeding* was characterised by the whale shark swimming quickly through food rich areas with their mouth open, often with the upper jaw, dorsal and caudal fin visible above the water (Motta et al, 2009). *Passive ram filter feeding* was designated as the shark moving slowly through the water with mouth partially open but with no pumping of the gills taking place (Taylor, 2007). *Suction feeding* was determined when a whale shark remained stationary in the water in a vertical position repeatedly gulping (Heyman et al, 2001; Nelsen & Eckhert, 2007). If any other unusual types of behaviour were observed these were noted.

If a shark had any unusual features such as a tag or visible injuries these were documented. Injuries have been classified into several categories according to Speed et al. (2008). The categories were *abrasions*, *lacerations*, *nicks*, *bites*, *blunt trauma*, *amputations* and 'other'

which were wounds that did not fit into any of the other categories (Figure 4). The likely cause of these injuries was noted.



**Figure 4.** Examples of whale shark injuries (1. Abrasion 2. Laceration 3. Bite 4. Amputation).

The characteristics of five different whale shark aggregations were analysed with data taken from the Wildbook for Whale Sharks online database (<https://www.whaleshark.org/>). These five sites- St Helena; the Maldives; Ningaloo reef, Australia; Isla Mujeres, Mexico; Mahe Island, the Seychelles- were chosen as they are the most well known and longest researched aggregations. Chi square ( $X^2$ ) tests were used to compare the occurrence of males and females in each aggregation. Significance was accepted at  $p < 0.05$ . All analyses were conducted using statistical package SPSS.

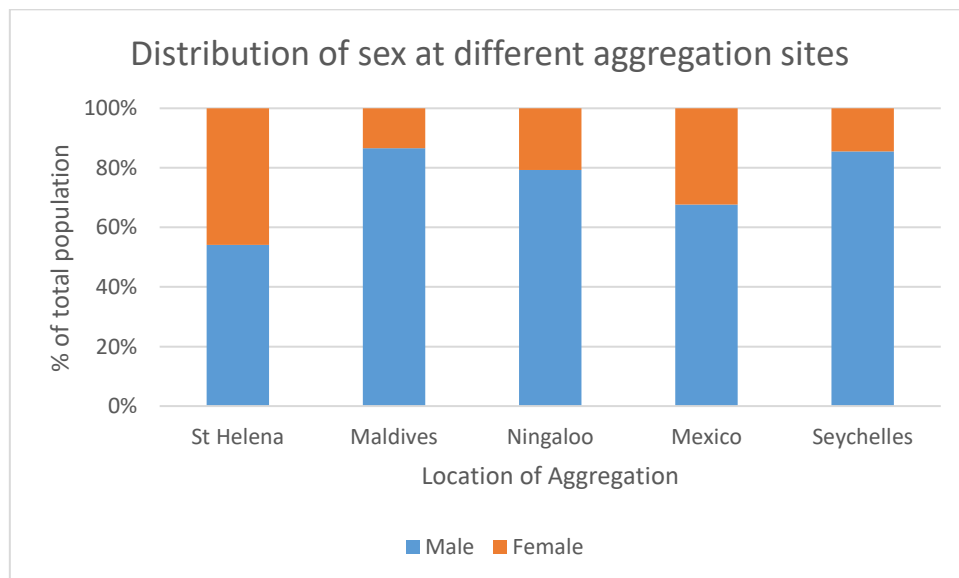
## Results

Of the five aggregations, four showed a male bias with the majority of the males being juvenile (Table 1). Only the St Helena aggregation had a more even ratio of males to females, and the males were almost exclusively mature ( $n=328$ , male =156, juvenile male=1) (Figure 5).

**Table 1:** Aggregation numbers at selected sites, sex and mean total length.

Aggregation	Total Number of Individuals Identified	Male	Female	Unknown	Mean Total Length
St Helena	328	157	133	38	7.63
Maldives	315	194	30	78	5.58
Ningaloo	7231	2257	590	4384	5.5
Mexico	5986	1351	645	3990	8.24
Seychelles	424	259	44	121	5.59

The mean total length of sharks in all aggregations was less than 8 metres, except at the Mexico site where mean length was 8.24 metres (Table 1). Whale sharks are considered to be mature when 9 metres long (Norman and Stevens, 2007) but visual observations of the claspers of the St Helena aggregation suggest that 156 males were mature, with only one being immature. Of all females observed (n=133), seven were thought to be gravid through visual observation. Analysis of the aggregations resulted in a low p-value, indicating that the variables are independent from each other suggesting that the sex ratios were related to the locations ( $X^2 = 182.8$ ,  $df = 4$ ,  $p = <0.001$ ).



**Figure 5:** Sex distribution at the different aggregation sites

Two sites of similar aggregation numbers and both within MPAs - St Helena and Maldives - were used to compare injury rates likely to have been caused by boat strikes (*abrasions*,

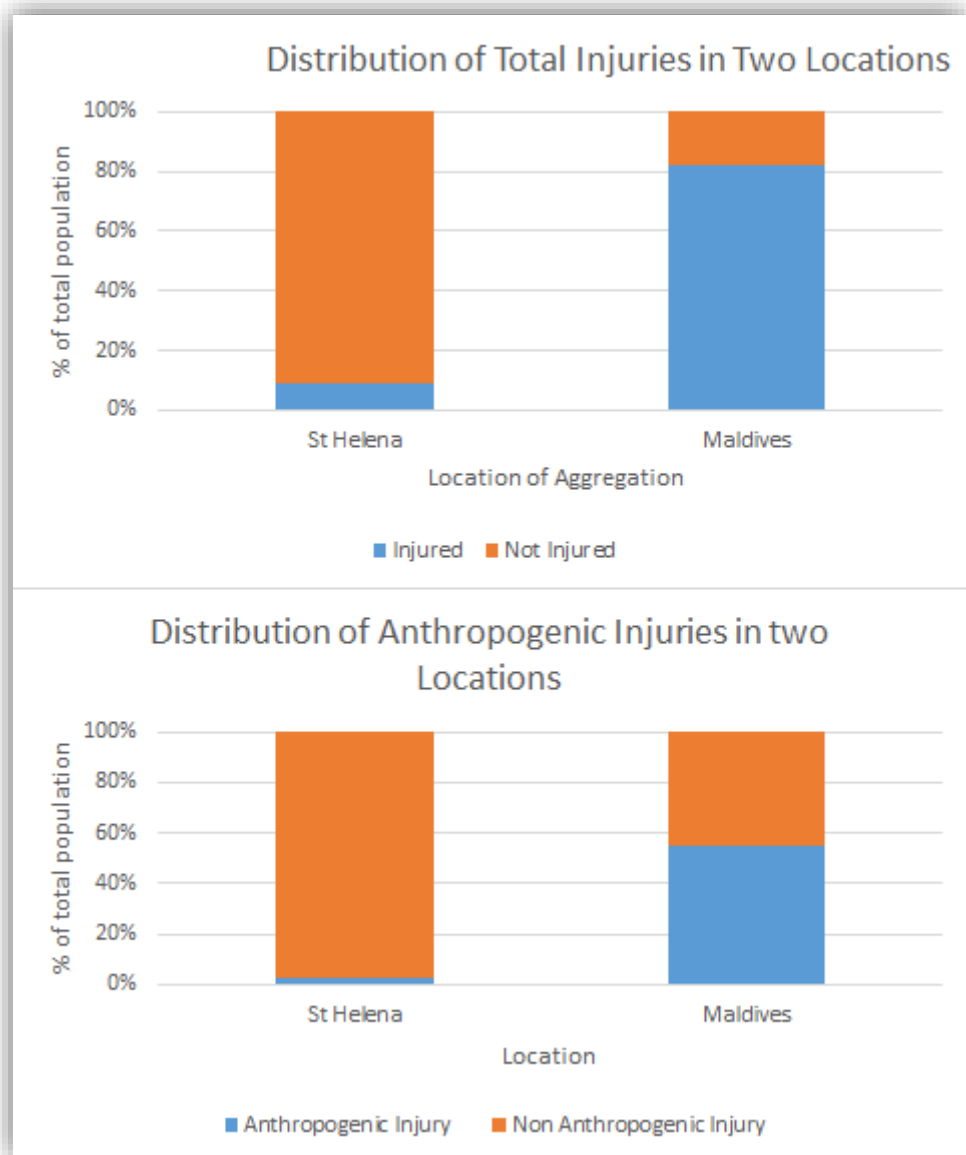
*lacerations, blunt trauma, and amputations*). St Helena has an undeveloped tourism industry and limited capacity for ecotourism with whale sharks. South Ari atoll in the Maldives has very high levels of tourism, with whale shark viewing trips especially popular (Table 2).

**Table 2:** Number of sharks bearing injuries likely to be caused by boat strikes and number of tourist boats at two locations

Aggregation	St Helena	Maldives
No of Tourist Operators	4	36
Injured	30	259

The number of tourist boats active in the MPAs was far higher in the Maldives (n=36) compared to St Helena (n=4) with the number of sharks observed bearing injuries likely to be caused by boat strikes in Maldives was much higher than in St Helena.

54.9% (n=315) of the sharks identified in the Maldives bore injuries consistent with boat strikes compared to 2.4% (n=328) of sharks in St Helena (Figure 6). The analysis suggests that the data isn't independent from each other and it is related to another factor, for example the number of boats. ( $X^2 = 346.8$ ,  $df = 4$ ,  $p = <0.001$ ) which shows a highly significant result.



**Figure 6:** Distribution of total injuries distribution of total anthropogenic injuries in two locations.

**Discussion**

**Importance of the St Helena whale shark aggregation**

The composition of whale sharks at each aggregation site varies in both sex and size, with many sites showing a juvenile male bias (Stewart et al 2007; Sequiera et al, 2011; Ketchum et al, 2012). These aggregations are associated with near-shore, seasonally abundant food

sources (Rohner et al, 2013). These large feeding events may aid growth, allowing juveniles to receive enough nutrients to achieve their full adult size (Rowat et al, 2012). Although nutrient upwellings are linked to abundant food sources (Rohner et al, 2013), the identification of these coastal aggregations is as likely to be a product of human behaviour- people are more likely to engage in water activities in near-shore, warm seas so are more likely to encounter animals there- as behaviour of the sharks. Tagging data show that juveniles spend more time in coastal waters near the surface than mature sharks who move offshore (Ramirez-Macias et al, 2017) so it is rational that most known aggregations are of juveniles. These aggregation sites are important to researchers as they allow whale sharks to be studied relatively easily compared to the challenges of studying highly mobile marine animals in the open ocean. However, it is difficult to draw conclusions about a species from limited cohorts, seasonally, in only a part of their habitat.

A whale shark may be capable of traversing the entire globe in two to four years (Sequiera et al, 2011; Beckley et al, 1997) allowing for the possibility of a panmictic global population (Sequiera et al, 2011; Rowat et al, 2012). The very limited genetic diversity recorded between global aggregation sites supports this assertion (Schmidt et al, 2009). We know that the same individuals have been found at single aggregation sites year after year using photo identification but to date there is no record of an individual being identified away from the aggregation at which it was first identified. So although observing movements over temporal and spatial scales can provide estimates of populations' size and distribution (Meekan et al, 2006; Holmberg et al, 2008), to advance our understanding of whale sharks it is important to locate the other components of the putative panmictic population.

The St Helena whale shark aggregation reported here is therefore considered to be significant because of its 46:54 female to male ratio, because almost all of the individuals were adults and because of the 133 female sharks observed in St Helena, seven were determined to be gravid. Ramirez-Macias et al (2017) suggested that gravid females move in to pelagic waters and there is some evidence of female sharks having a more pelagic diet

(Borrell et al, 2011). This is in keeping with the location of St Helena, surrounded by deep ocean- bathymetrically similar to the Galapagos Islands where gravid females have also been observed (Hearn et al, 2016).

*R. typus* courtship and mating behaviour is poorly understood. A few observations of male and female whale shark interactions - the nose-to-tail following, parallel and echelon swimming - documented by Martin (2007) may be similar to those observed in basking sharks by Sims et al (2000). These are consistent with other shark courtship behaviours in aggregations (Martin, 2007). On two occasions in St Helena in 2016, a lone female appeared to be stationary in the water about 5 m below the surface in an inverted arc position with head and caudal higher than the belly (Pers. Obs., St Helena 2016). After a few minutes in this position, a number of male sharks approached the female. In the absence of abundant food, usually when two whale sharks meet they circle each other before swimming away but the female in these two instances maintained her position while the males swam around her. Eventually the female moved away followed by the males. This may be the first time this behaviour has been documented in whale sharks although fellow Orectolobiformes - nurse sharks (*Ginglymostoma cirratum*) - have been observed adopting a similar position prior to mating (Carrier et al, 1994). Similarly, female sand tiger sharks (*Carcharias taurus*) have also been observed to stop all forward movement in the water just below the surface in a posture documented as 'stalling' before mating was observed between males and females (Pratt & Carrier, 2001). Reports from St Helena fishermen of "belly to belly" contact between whale sharks, interpreted as mating behaviour (Clingham et al, 2016) have not been verified and could be attributed to other behaviour, such as the sharks competing for by-catch being jettisoned by the fishermen. However, in combination these observations suggest that St Helena could be a significant research location for whale shark reproduction.

**Threats to whale sharks – injury rates likely resulting from boat strikes in aggregations with varying levels of ecotourism**

Because whale sharks are harmless to humans and can be found predictably, in warm waters, in relatively large numbers targeted human interactions are increasing. Governments are often keen to develop ecotourism as it can generate substantial revenue. A study of whale shark tourism in the Maldives reported between 72,000 – 78,000 tourists participated in whale shark excursions at South Ari atoll between 2013 and 2014 generating between US\$ 7.8 and US\$ 9.4 million in revenue (Cagua et al, 2014).

Whale shark tourism in St Helena is limited. Approximately 3,600 tourists visit the island each year, there are only four accredited marine tourism operators, and there a very low numbers of visiting vessels (SHG State of the Island, 2015). Local ordinances mandate standardised briefings are given to tourists; place limitations on boat speeds; mandate that only one vessel is permitted within 100 m of any whale shark and a maximum of 8 people are permitted in the water at any time. After 45 minutes of interaction the shark has to be left alone. This is supported by a public information campaign, and the small community and single harbour make monitoring adherence to licence conditions relatively easy (SHG, 2016).

In contrast, 1.9 million tourists visit the Maldives each year and the author estimates that at least 36 boats conduct whale shark tourist trips at any one time in the South Ari MPA. There have been instances where a larger number of boats have been recorded. The vessels come from multiple harbours and resorts and although there are best practise guidelines in place there is no enforcement and operators are not licenced.

Of the 328 sharks recorded at St Helena 8, 2.4% of the aggregation, bore injuries consistent with boat strikes and these were healed scars observed suggesting they didn't happen recently, or necessarily around St Helena. Conversely in South Ari in the Maldives 173 of the 315 sharks identified (54.9%) bore these injuries, the majority being fresh. The analysis suggests that this is linked to a higher number of tourist vessels targeting the Maldives aggregation. Other factors may contribute towards the different injury rates: the Maldives is

an archipelago with far higher rates of commercial boat traffic than St Helena - although these vessels do not regularly transit the MPA the sharks may be being injured elsewhere.

The behaviour of the predominantly juvenile sharks in the Maldives may increase the likelihood of them coming in to contact with boats as they may spend more time near the surface than the mature sharks encountered at St Helena (Ramirez-Macias et al, 2017). However, this argues for tighter regulation of vessels in areas where the more vulnerable juveniles aggregate.

Aside from the direct injury to the shark, open wounds could leave the animal less resilient to disease and parasites, and may affect its foraging ability and metabolism. Whale sharks may also become excluded from important habitats as they seek to avoid higher disturbance levels caused by unregulated ecotourism (Trujillo-Córdova et al, 2016; Quiros, 2007). In the Maldives it has been observed that whale sharks spend less time on the surface when many people enter the water with them (MWSRP, 2017). Whale sharks are speculated to stay at the surface to warm up and recover after a deep dive, a reduced recovery time may have detrimental effects on the shark.

Whale shark aggregations are known to follow seasonally abundant food sources (Rohner et al, 2013) and it is possible that entire aggregations are able to relocate without detriment to the sharks. For example during La Nina years, Ningaloo reef experiences higher numbers of whale sharks than in El Nino Southern Oscillation years (Stevens, 2006). However, if the whale shark aggregations do relocate it would cause the site specific ecotourism industries built around them to collapse.

## **Conclusion**

The behavioural ecology of mature whale sharks is poorly understood. Projections and assumptions made from studying the largely male, juvenile aggregations in isolated locations tell us little about this far ranging and long-lived fish. Therefore, the unusual characteristics of the St Helena whale shark aggregation – mature adults, near equal sex ratio and gravid

females- combined with the proximity to deep pelagic water, and the observed male and female interactions suggests it could be of particular scientific interest. A dedicated, full time research facility should be considered as the remoteness of the island and its relative inaccessibility make regular research by visiting teams challenging.

The comparatively high injury rates recorded in the Maldives archipelago are at least in part due to poorly regulated ecotourism. The impact of this on the animals is unknown but if they are excluded from an important habitat the survivorship and fecundity of the juveniles could be negatively affected. And if an aggregation moves to a different location the industry that depends on the whale sharks could fail. The St Helena Government should heed these lessons and ensure that when commercial flights to the island start in 2018, bringing increased tourism, they continue to protect their whale shark aggregation.

## References

- Acuña-Marrero, D., Jiménez, J., Smith, F., Doherty, P., Hearn, A., Green, J., Paredes-Jarrín, J., and Salinas-de-León, P. (2014). Whale Shark (*Rhincodon typus*) Seasonal Presence, Residence Time and Habitat Use at Darwin Island, Galapagos Marine Reserve. *PLoS ONE*, 9(12), e115946. Available at: [Accessed: 4 June 2017].
- Akhilesh, K., Shanis, C., White, W., Manjebrayakath, H., Bineesh, K., Ganga, U., Abdussamad, E., Gopalakrishnan, A., and Pillai, N. (2012). Landings of whale sharks *Rhincodon typus* Smith, 1828 in Indian waters since protection in 2001 through the Indian Wildlife (Protection) Act, 1972. *Environmental Biology of Fishes*, 96(6), 713-722. Available at: [Accessed: 6 May 2017].
- Alerstam, T., Hedenstrom, A., and Akesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, 103(2), 247-260.
- Amande, M., Chassot, E., Chavance, P., Murua, H., de Molina, A., and Bez, N. (2012). Precision in bycatch estimates: the case of tuna purse-seine fisheries in the Indian Ocean. *ICES Journal of Marine Science*, 69(8), 1501-1510. Available at: [Accessed: 14 June 2017].
- Anandhakumar, C., Dhinakar Raj, G., Tirumurugaan, A., Raja, K., Kumanan, A., and Uma, K. (2012). Mating behaviour and breeding of the grey bamboo shark, *Chiloscyllium griseum* Muller & Henle, 1838 in captivity. *Indian Journal of Fisheries*, [Online]. Vol.59(3), pp.149-152. Available at: <http://epubs.icar.org.in/ejournal/index.php/IJF/issue/archive>. [Accessed: 4 June 2017].
- Anderson, K (2017). *Whalesharks*. [Online]. 2017. Coralbay.org. Available at: <http://www.coralbay.org/whalesk.htm>. [Accessed: 21 May 2017].
- Andrzejaczek, S., Meeuwig, J., Rowat, D., Pierce, S., Davies, T., Fisher, R., and Meekan, M. (2016). Establishing the ecological connectivity of whale shark aggregations across the Indian Ocean – a photo-identification approach. *QScience Proceedings. The 4th International Whale Shark Conference, 16–18 May 2016, Doha, Qatar*, [Online]. Available at: <http://www.qscience.com/toc/qproc/2016/2>. [Accessed: 29 January 2017].
- Anon (2017). *QScience.com | QScience Proceedings - Most Cited Papers*. [Online]. 2017. Qscience.com. Available at: <http://www.qscience.com/toc/qproc/2016/2>. [Accessed: 2 March 2017].
- Arzoumanian, Z., Holmberg, J., and Norman, B. (2005). An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. *Journal of Applied Ecology*, 42(6), 999-1011. Available at: [Accessed: 14 May 2017].
- Beckley, L., Cliff, G., Smale, M., and Compagno, L. (1997). Recent strandings and sightings of whale sharks in South Africa. *Environmental Biology of Fishes*, 50(3), 343–348. Available at: [Accessed: 1 June 2017].
- Bishop, J. and Abdul-Ghaffar, A. (1993). Whale shark observations off Kuwait's coast in 1992. *Journal of Fish Biology*, 43(6), 939-940. Available at: [Accessed: 3 February 2017].
- Bombay Research Centre of Central Marine Fisheries Research Institute, India (1986). *Whale Shark: Endangered or Vulnerable?*. Technical and Extension Series. Cochin, India: Central Marine Fisheries Research Institute. Available at: [Accessed: 28 May 2017].

- Borrell, A., Aguilar, A., Gazo, M., Kumarran, R., and Cardona, L. (2011). Stable isotope profiles in whale shark (*Rhincodon typus*) suggest segregation and dissimilarities in the diet depending on sex and size. *Environmental Biology of Fishes*, 92(4), 559-567. Available at: [Accessed: 18 May 2017].
- Bradshaw, C., Fitzpatrick, B., Steinberg, C., Brook, B., and Meekan, M. (2008). Decline in whale shark size and abundance at Ningaloo Reef over the past decade: The world's largest fish is getting smaller. *Biological Conservation*, 141(7), 1894-1905.
- Bradshaw, C., Mollet, H., and Meekan, M. (2007). Inferring population trends for the world's largest fish from mark recapture estimates of survival. *Journal of Animal Ecology*, 76(3), 480-489. Available at: [Accessed: 27 February 2017].
- Brillinger, D. and Stewart, B. (2010). Stochastic modelling of particle movement with application to marine biology and oceanography. *Journal of Statistical Planning and Inference*, 140(12), 3597-3607. Available at: [Accessed: 9 June 2017].
- Brunnschweiler, J., Baensch, H., Pierce, S., and Sims, D. (2009). Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. *Journal of Fish Biology*, 74(3), 706-714. Available at: [Accessed: 18 April 2017].
- Catarci, C. (2004). *World Markets And Industry of Selected Commercially Exploited Aquatic Species With an International Conservation Profile*. 1st edn. Rome: FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS.
- Cagua, E., Collins, N., Hancock, J., and Rees, R. (2014). Whale shark economics: a valuation of wildlife tourism in South Ari Atoll, Maldives. *PeerJ*, 2, e515. Available at: [Accessed: 19 January 2017].
- Cárdenas-Torres, N., Enríquez-Andrade, R., and Rodríguez-Dowdell, N. (2007). Community-based management through ecotourism in Bahía de los Angeles, Mexico. *Fisheries Research*, 84(1), 114-118. Available at: [Accessed: 30 March 2017].
- Carrier, J., Pratt, Jr, H., and Martin, L. (1994). Group Reproductive Behaviours in Free-Living Nurse Sharks, *Ginglymostoma cirratum*. *Copeia*, [Online]. 3(Aug. 17, 1994), pp. 646-656. Available at: [http://www.jstor.org/stable/1447180?seq=1#page\\_scan\\_tab\\_contents](http://www.jstor.org/stable/1447180?seq=1#page_scan_tab_contents). [Accessed: 8 June 2017].
- Castro, A., Stewart, B., Wilson, S., Hueter, R., Meekan, M., Motta, P., Bowen, B., and Karl, S. (2007). Population genetic structure of Earth's largest fish, the whale shark (*Rhincodon typus*). *Molecular Ecology*, 16(24), 5183-5192. Available at: [Accessed: 16 March 2017].
- Catlin, J., Jones, T., Norman, B., and Wood, D. (2009). Consolidation in a wildlife tourism industry: the changing impact of whale shark tourist expenditure in the Ningaloo coast region. *International Journal of Tourism Research*, n/a-n/a. Available at: [Accessed: 3 April 2017].
- Catlin, J., Jones, T., and Jones, R. (2012). Balancing commercial and environmental needs: licensing as a means of managing whale shark tourism on Ningaloo reef. *Journal of Sustainable Tourism*, 20(2), 163-178.
- Chang, W., Leu, M., and Fang, L. (1997). Embryos of the Whale Shark, *Rhincodon typus*: Early Growth and Size Distribution. *Copeia*, [Online]. 2(May 13, 1997), pp. 444-446. Available at: [http://www.jstor.org/stable/1447769?seq=1#page\\_scan\\_tab\\_contents](http://www.jstor.org/stable/1447769?seq=1#page_scan_tab_contents). [Accessed: 3 February 2017].

- Chen, V. and Phipps, M. (2002). *Management and Trade of Whale Sharks in Taiwan*. Taipei: TRAFFIC East Asia. Available at: [Accessed: 19 June 2017].
- CITES (2017). *Whale Shark* | Cites.org. Available at: [https://cites.org/eng/gallery/species/fish/whale\\_shark.html](https://cites.org/eng/gallery/species/fish/whale_shark.html). [Accessed: 3 May 2017].
- Cliff, G., Anderson-Read, M., Aitken, A., Charter, G., and Peddemors, V. (2007). Aerial census of whale sharks (*Rhincodon typus*) on the northern KwaZulu-Natal coast, South Africa. *Fisheries Research*, 84(1), 41-46. Available at: [Accessed: 23 March 2017].
- Clingham, Elizabeth et al. "Evidence That St. Helena Island Is An Important Multi-Use Habitat For Whale Sharks, *Rhincodon Typus*, With The First Description Of Putative Mating In This Species". *PeerJ* (2016): n. pag. Web. 13 Mar. 2017.
- Cochran, J., Hardenstine, R., Braun, C., Skomal, G., Thorrold, S., and Berumen, M. (2016). Population structure of a Red Sea whale shark aggregation. *QScience Proceedings (The 4th International Whale Shark Conference) 2016:iwsc4.12*, [Online]. Available at: <http://www.qscience.com/toc/qproc/2016/2>. [Accessed: 2 May 2017].
- Colman, J. (1997). A review of the biology and ecology of the whale shark. *Journal of Fish Biology*, 51(6), 1219-1234. Available at: [Accessed: 22 April 2017].
- Compagno, L. (1984). *FAO species catalogue Vol 4, Part 2: Sharks of the World*. Rome: United Nations Development Programme.
- Compagno, L. (2001). *Sharks of the world*. 1st edn. Rome: Food and Agriculture Organization of the United Nations.
- Couturier, L., Rohner, C., Richardson, A., Pierce, S., Marshall, A., Jaïne, F., Townsend, K., Bennett, M., Weeks, S., and Nichols, P. (2013). Unusually High Levels of n-6 Polyunsaturated Fatty Acids in Whale Sharks and Reef Manta Rays. *Lipids*, 48(10), 1029-1034. Available at: [Accessed: 17 May 2017].
- Davis, D., Banks, S., Birtles, A., Valentine, P., and Cuthill, M. (1997). Whale sharks in Ningaloo Marine Park: managing tourism in an Australian marine protected area. *Tourism Management*, 18(5), 259-271. Available at: [Accessed: 4 March 2017].
- de la Parra-Venegas, R., Galván-Pastoriza, B., Pierce, S., and Sosa-Nishizaki, O. (2016). Scarring estimation in the largest whale shark aggregation. *QScience Proceedings (The 4th International Whale Shark Conference)*, [Online]. Available at: <http://www.qscience.com/doi/pdf/10.5339/qproc.2016.iwsc4.14>. [Accessed: 13 June 2017].
- de la Parra Venegas, R., Hueter, R., González Cano, J., Tyminski, J., Gregorio Remolina, J., Maslanka, M., Ormos, A., Weigt, L., Carlson, B., and Dove, A. (2011). An Unprecedented Aggregation of Whale Sharks, *Rhincodon typus*, in Mexican Coastal Waters of the Caribbean Sea. *PLoS ONE*, 6(4), e18994. Available at: [Accessed: 11 May 2017].
- Donati, G., Rees, R., Hancock, J., Jenkins, T., Shameel, I., Hindle, K., Zareer, I., Childs, A., and Cagua, F. (2016). New insights into the South Ari atoll whale shark, *Rhincodon typus*, aggregation. *QScience Proceedings (The 4th International Whale Shark Conference)*, [Online]. Available at: <http://www.qscience.com/toc/qproc/2016/2>. [Accessed: 5 March 2017].
- Dove, A., Arnold, J., and Clauss, T. (2010). Blood cells and serum chemistry in the world's largest fish: the whale shark *Rhincodon typus*. *Aquatic Biology*, 9(2), 177-183. Available at: [Accessed: 7 May 2017].

- Duffy, C. (2002). Distribution, seasonality, lengths, and feeding behaviour of whale sharks (*Rhincodon typus*) observed in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research*, 36(3), 565-570. Available at: [Accessed: 19 May 2017].
- Eckert, S. and Stewart, B. (2001). *Environmental Biology of Fishes*, 60(1/3), 299-308. Available at: [Accessed: 24 April 2017].
- Eckert, S., Dolar, L., Kooyman, G., Perrin, W., and Rahman, R. (2002). Movements of whale sharks (*Rhincodon typus*) in South-east Asian waters as determined by satellite telemetry. *Journal of Zoology*, 257(1), 111-115. Available at: [Accessed: 4 April 2017].
- Environmental Management Division, St Helena Government (2016). *Whale Sharks St Helena*. [Online]. Available at: <http://www.sainthelena.gov.sh/wp-content/uploads/2013/07/whale-shark-leaflet.pdf>. [Accessed: 4 February 2017].
- Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A. and Musick, J.A. (comp. and ed.). 2005. *Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes. Status Survey*. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. x + 461 pp.
- Gifford, A., Compagno, L., Levine, M., and Antoniou, A. (2007). Satellite tracking of whale sharks using tethered tags. *Fisheries Research*, 84(1), 17-24. Available at: [Accessed: 7 April 2017].
- Graham, R. and Roberts, C. (2007). Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. *Fisheries Research*, 84(1), 71-80. Available at: [Accessed: 11 May 2017].
- Graham, R., Roberts, C., and Smart, J. (2006). Diving behaviour of whale sharks in relation to a predictable food pulse. *Journal of The Royal Society Interface*, 3(6), 109-116. Available at: [Accessed: 6 April 2017].
- Gudger, E. (1915). *Natural history of the whale shark, Rhineodon typus Smith. Zoologica, Scientific Contributions of the New York Zoological Society*. 1st edn. New York: New York Zoological Society.
- Hammerschlag, N., Gallagher, A., and Lazarre, D. (2011). A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology*, 398(1-2), 1-8. Available at: [Accessed: 11 May 2017].
- Haskell, P., McGowan, A., Westling, A., Méndez-Jiménez, A., Rohner, C., Collins, K., Rosero-Caicedo, M., Salmond, J., Monadjem, A., Marshall, A., and Pierce, S. (2014). Monitoring the effects of tourism on whale shark *Rhincodon typus* behaviour in Mozambique. *Oryx*, 49(03), 492-499. Available at: [Accessed: 6 June 2017].
- Hearn, A., Espinoza, E., Green, J., Acuña-Marrero, D., and Ryan, J. (2016). Association of adult female whale sharks with open ocean and coastal upwelling frontal systems in the Eastern Tropical Pacific. *QScience Proceedings (The 4th International Whale Shark Conference)*, [Online]. Available at: <http://www.qscience.com/doi/pdf/10.5339/qproc.2016.iwsc4.24>. [Accessed: 14 May 2017].
- Hernández-Nava, M. and Álvarez-Borrego, S. (2013). Zooplankton in a whale shark (*Rhincodon typus*) feeding area of Bahía de los Ángeles (Gulf of California). *Hidrobiologica*, [Online]. 23(2), 198-208. Available at:

[http://www.scielo.org.mx/scielo.php?script=sci\\_serial&pid=0188-8897&lng=es&nrm=iso](http://www.scielo.org.mx/scielo.php?script=sci_serial&pid=0188-8897&lng=es&nrm=iso). [Accessed: 23 May 2017].

- Hueter, R., Heupel, M., Heist, E., and Keeney, D. (2004). Evidence of Philopatry in Sharks and Implications for the Management of Shark Fisheries. *Journal of Northwest Atlantic Fishery Science*, 35, 239-247.
- Heyman, W., Graham, R., Kjerfve, B., and Johannes, R. (2001). Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series*, 215, 275-282.
- Hobbs, J., Frisch, A., Hamanaka, T., McDonald, C., Gilligan, J., and Neilson, J. (2009). Seasonal aggregation of juvenile whale sharks (*Rhincodon typus*) at Christmas Island, Indian Ocean. *Coral Reefs*, 28(3), 577-577. Available at: [Accessed: 9 June 2017].
- Holden, M. and Raitt, D. (1974). *Manual of fisheries science - Part 2 - Methods of Resource Investigation and their Application*. 1st edn. Rome: Food and Agriculture Organization of the United Nations, 1974.
- Holmberg, J., Norman, B., and Arzoumanian, Z. (2009). Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. *Endangered Species Research*, 7, 39-53. Available at: [Accessed: 9 May 2017].
- Holmberg, J., Norman, B., and Arzoumanian, Z. (2008). Robust, Comparable Population Metrics Through Collaborative Photo-monitoring of Whale sharks *Rhincodon Typus*. *Ecological Applications*, 18(1), 222-233.
- Hsu, H., Joung, S., Liao, Y., and Liu, K. (2007). Satellite tracking of juvenile whale sharks, *Rhincodon typus*, in the Northwestern Pacific. *Fisheries Research*, 84(1), 25-31. Available at: [Accessed: 3 May 2017].
- Hussey, N., MacNeil, M., and Fisk, A. (2010). The requirement for accurate diet-tissue discrimination factors for interpreting stable isotopes in sharks. *Hydrobiologia*, 654(1), 1-5. Available at: [Accessed: 10 May 2017].
- IUCN (2017). *Discover the Whale Shark!*. [Online]. 2017. IUCN Red List 50. Available at: <http://support.iucnredlist.org/species/whale-shark>. [Accessed: 5 May 2017].
- Jarman, S. and Wilson, S. (2004). DNA-based species identification of krill consumed by whale sharks. *Journal of Fish Biology*, 65(2), 586-591.
- John, S. (2010). Observation of a Whale Shark *Rhincodon typus* (Orectolobiformes: Rhincodontidae) in the offshore waters of Rushikulya, Orissa, India. *Journal of Threatened Taxa*, 2(5), 896-897. Available at: [Accessed: 9 June 2017].
- Jonahson, M. and Harding, S. (2007). Occurrence of whale sharks (*Rhincodon typus*) in Madagascar. *Fisheries Research*, 84(1), 132-135.
- Joung, S., Chen, C., Clark, E., Uchida, S., and Huang, W. (1996). The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one ?megamamma? supreme. *Environmental Biology of Fishes*, 46(3), 219-223. Available at: [Accessed: 2 May 2017].
- Ketchum, J., Galván-Magaña, F., and Klimley, A. (2012). Segregation and foraging ecology of whale sharks, *Rhincodon typus*, in the southwestern Gulf of California. *Environmental Biology of Fishes*, 96(6), 779-795. Available at: [Accessed: 20 April 2017].

- Karbhari, J.P., Josekutty, C.J. (1986). On the largest whale shark *Rhincodon typus* Smith landed alive at Cuffe Parade, Bombay. *Mar. Fish. Inform. Serv. Tech. Inform. Ser.*, 66 (1986), pp. 31-35
- Khan, T., Quadir, D., Murty, T., Kabir, A., Aktar, F., and Sarker, M. (2002). Relative Sea Level Changes in Maldives and Vulnerability of Land Due to Abnormal Coastal Inundation. *Marine Geodesy*, 25(1-2), 133-143. Available at: [Accessed: 14 June 2017].
- Klimley, A. (2013). *The biology of sharks and rays*. 1st edn. Chicago: The University of Chicago Press.
- Klimley, A. and Butler, S. (1988). Immigration and emigration of a pelagic fish assemblage to seamounts in the Gulf of California related to water mass movements using satellite imagery. *Marine Ecology Progress Series*, 49, 11-20.
- Kukuyev, E. (1996). The new finds in recently born individuals of the whale shark *Rhincodon typus* (Rhiniodontidae) in the Atlantic Ocean. *Journal of Ichthyology*, 36(2), 203. Available at: [Accessed: 19 June 2017].
- Kumari, B. and Raman, M. (2010). Whale shark habitat assessments in the northeastern Arabian Sea using satellite remote sensing. *International Journal of Remote Sensing*, 31(2), 379-389.
- Marshall, A. and Pierce, S. (2012). The use and abuse of photographic identification in sharks and rays. *Journal of Fish Biology*, 80(5), 1361-1379. Available at: [Accessed: 9 May 2017].
- Martin, R. (2007). A review of behavioural ecology of whale sharks (*Rhincodon typus*). *Fisheries Research*, 84(1), 10-16. Available at: [Accessed: 12 May 2017].
- Martin, R. (2007). A review of shark agonistic displays: comparison of display features and implications for shark–human interactions. *Marine and Freshwater Behaviour and Physiology*, 40(1), 3-34.
- Martin, R. (2007). A review of shark agonistic displays: comparison of display features and implications for shark–human interactions. *Marine and Freshwater Behaviour and Physiology*, 40(1), 3-34. Available at: [Accessed: 19 June 2017].
- Martin, A (2017). *Hearing and Vibration Detection*. [Online]. 2017. ElasmO-research.org. Available at: [http://www.elasmO-research.org/education/white\\_shark/hearing.htm](http://www.elasmO-research.org/education/white_shark/hearing.htm). [Accessed: 20 May 2017].
- Mau, R. (2008). Managing for Conservation and Recreation: The Ningaloo Whale Shark Experience. *Journal of Ecotourism*, 7(2&3), 208.
- McKinney, J., Hoffmayer, E., Wu, W., Fulford, R., and Hendon, J. (2012). Feeding habitat of the whale shark *Rhincodon typus* in the northern Gulf of Mexico determined using species distribution modelling. *Marine Ecology Progress Series*, 458, 199-211. Available at: [Accessed: 5 June 2017].
- Meekan, M., Bradshaw, C., Press, M., McLean, C., Richards, A., Quasnichka, S., and Taylor, J. (2006). Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series*, 319, 275-285.
- Moazzam, M., Osmany, H., Nawaz, R., and Ayub, S. (2016). Distribution, abundance and mortality of whale sharks (*Rhincodon typus*) in coastal and offshore waters of Pakistan (Northern Arabian Sea): Review of a ten year study with information on the successful release of whale sharks entangled in fishing gear. *QScience Proceedings*, [Online].

Available at: <http://www.qscience.com/doi/pdf/10.5339/qproc.2016.iwsc4.37>. [Accessed: 7 June 2017].

- Motta, P., Maslanka, M., Hueter, R., Davis, R., de la Parra, R., Mulvany, S., Habegger, M., Strother, J., Mara, K., Gardiner, J., Tyminski, J., and Zeigler, L. (2010). Feeding anatomy, filter-feeding rate, and diet of whale sharks *Rhincodon typus* during surface ram filter feeding off the Yucatan Peninsula, Mexico. *Zoology*, 113(4), 199-212. Available at: [Accessed: 3 May 2017].
- Myrberg, Jr., A. (2001). The acoustical biology of elasmobranchs. *Environmental Biology of Fishes*, 60(1/3), 31-46.
- Nelson, J. and Eckert, S. (2007). Foraging ecology of whale sharks (*Rhincodon typus*) within Bahía de Los Angeles, Baja California Norte, México. *Fisheries Research*, 84(1), 47-64. Available at: [Accessed: 3 May 2017].
- Norman, B. (2016). Are we losing the battle to save the biggest fish in the sea – and can we turn it around?. *QScience Proceedings (The 4th International Whale Shark Conference)*, [Online]. Available at: <http://www.qscience.com/doi/pdf/10.5339/qproc.2016.iwsc4.39>. [Accessed: 9 June 2017].
- Norman, B. and Stevens, J. (2007). Size and maturity status of the whale shark (*Rhincodon typus*) at Ningaloo Reef in Western Australia. *Fisheries Research*, 84(1), 81-86. Available at: [Accessed: 5 April 2017].
- O'Sullivan, J. and Mitchell, T. (2000). A fatal attack on a whale shark *Rhincodon typus*, by killer whales *Orcinus orca* off Bahia de Los Angeles, Baja California. *American Society of Ichthyologists and Herpetologists 80th Annual Meeting/American Elasmobranch Society (ASIH/AES), La Paz, Mexico.*, Available at: [Accessed: 4 June 2017].
- Perry, C. and Morgan, K. (2017). Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. *Scientific Reports*, 7, 40581. Available at: [Accessed: 8 June 2017].
- Pierce, S., Méndez-Jiménez, A., Collins, K., Rosero-Caicedo, M., and monadjem, A. (2010). Developing a Code of Conduct for whale shark interactions in Mozambique. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 20(7), 782-788. Available at: [Accessed: 23 April 2017].
- Pratt, Jr., H. and Carrier, J. (2001). *Environmental Biology of Fishes*, 60(1/3), 157-188. Available at: [Accessed: 7 June 2017].
- Pravin, P. (2000). Whale shark in the Indian coast – Need for conservation. *CURRENT SCIENCE, VOL. 79, NO. 3, 10 AUGUST 2000*, [Online]. 79(3), 310-315. Available at: <http://www.iisc.ernet.in/~currsci/aug102000/ga687.pdf>. [Accessed: 3 June 2017].
- Quiros, A. (2007). Tourist compliance to a Code of Conduct and the resulting effects on whale shark (*Rhincodon typus*) behavior in Donsol, Philippines. *Fisheries Research*, 84(1), 102-108.
- Ramírez-Macías, D., Queiroz, N., Pierce, S., Humphries, N., Sims, D., and Brunnschweiler, J. (2017). Oceanic adults, coastal juveniles: tracking the habitat use of whale sharks off the Pacific coast of Mexico. *PeerJ*, 5, e3271. Available at: [Accessed: 9 May 2017].
- Riley, M., Hale, M., Harman, A., and Rees, R. (2010). Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives Archipelago. *Aquatic Biology*, 8, 145-150. Available at: [Accessed: 5 February 2017].

- Rodríguez-Dowdell, N., Enríquez-Andrade, R., and Cárdenas-Torres, N. (2007). Property rights-based management: Whale shark ecotourism in Bahía de los Angeles, Mexico. *Fisheries Research*, 84(1), 119-127.
- Rohner, C., Pierce, S., Marshall, A., Weeks, S., Bennett, M., and Richardson, A. (2013). Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. *Marine Ecology Progress Series*, 482, 153-168. Available at: [Accessed: 29 April 2017].
- Rohner, C., Richardson, A., Prebble, C., Marshall, A., Bennett, M., Weeks, S., Cliff, G., Wintner, S., and Pierce, S. (2015). Laser photogrammetry improves size and demographic estimates for whale sharks. *PeerJ*, 3, e886. Available at: [Accessed: 16 May 2017].
- Rowat, D. and Brooks, K. (2012). A review of the biology, fisheries and conservation of the whale shark *Rhincodon typus*. *Journal of Fish Biology*, 80(5), 1019-1056. Available at: [Accessed: 25 March 2017].
- Rowat, D. and Engelhardt, U. (2007). Seychelles: A case study of community involvement in the development of whale shark ecotourism and its socio-economic impact. *Fisheries Research*, 84(1), 109-113. Available at: [Accessed: 19 May 2017].
- Rowat, D. and Gore, M. (2007). Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. *Fisheries Research*, 84(1), 32-40. Available at: [Accessed: 28 May 2017].
- Rowat, D., Gore, M., Baloch, B., Islam, Z., Ahmad, E., Ali, Q., Culloch, R., Hameed, S., Hasnain, S., Hussain, B., Kiani, S., Siddiqui, J., Ormond, R., Henn, N., and Khan, M. (2007). New records of neonatal and juvenile whale sharks (*Rhincodon typus*) from the Indian Ocean. *Environmental Biology of Fishes*, 82(3), 215-219. Available at: [Accessed: 1 June 2017].
- Rowat, D., Speed, C., Meekan, M., Gore, M., and Bradshaw, C. (2009). Population abundance and apparent survival of the vulnerable whale shark *Rhincodon typus* in the Seychelles aggregation. *Oryx*, 43(04), 591.
- Rowat, D. (2007). Occurrence of whale shark (*Rhincodon typus*) in the Indian Ocean: A case for regional conservation. *Fisheries Research*, 84(1), 96-101. Available at: [Accessed: 24 April 2017].
- Rowat, D., Meekan, M., Engelhardt, U., Pardigon, B., and Vely, M. (2006). Aggregations of juvenile whale sharks (*Rhincodon typus*) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes*, 80(4), 465-472. Available at: [Accessed: 16 April 2017].
- Schmidt, J., Schmidt, C., Ozer, F., Ernst, R., Feldheim, K., Ashley, M., and Levine, M. (2009). Low Genetic Differentiation across Three Major Ocean Populations of the Whale Shark, *Rhincodon typus*. *PLoS ONE*, 4(4), e4988.
- Sequeira, A., Mellin, C., Floch, L., Williams, P., and Bradshaw, C. (2014). Inter-ocean asynchrony in whale shark occurrence patterns. *Journal of Experimental Marine Biology and Ecology*, 450, 21-29. Available at: [Accessed: 1 May 2017].
- Sequeira, A., Mellin, C., Meekan, M., Sims, D., and Bradshaw, C. (2013). Inferred global connectivity of whale shark *Rhincodon typus* populations. *Journal of Fish Biology*, 82(2), 367-389. Available at: [Accessed: 1 May 2017].

- Sequeira, A., Mellin, C., Rowat, D., Meekan, M., and Bradshaw, C. (2011). Ocean-scale prediction of whale shark distribution. *Diversity and Distributions*, 18(5), 504-518. Available at: [Accessed: 3 May 2017].
- Sims, D., Southall, E., Quayle, V., and Fox, A. (2000). Annual social behaviour of basking sharks associated with coastal front areas. *Proceedings of the Royal Society B: Biological Sciences*, 267(1455), 1897-1904. Available at: [Accessed: 27 May 2017].
- Sleeman, J., Meekan, M., Wilson, S., Polovina, J., Stevens, J., Boggs, G., and Bradshaw, C. (2010). To go or not to go with the flow: Environmental influences on whale shark movement patterns. *Journal of Experimental Marine Biology and Ecology*, 390(2), 84-98. Available at: [Accessed: 3 May 2017].
- Smith, A. (1828). Descriptions of new or imperfectly known objects of the animal kingdom, found in the South of Africa. *South African Commercial Advertiser*, Column 4. Available at: [Accessed: 19 June 2017].
- Speed, C., Meekan, M., Rowat, D., Pierce, S., Marshall, A., and Bradshaw, C. (2008). Scarring patterns and relative mortality rates of Indian Ocean whale sharks. *Journal of Fish Biology*, 72(6), 1488-1503. Available at: [Accessed: 17 May 2017].
- SPC-OFP (2012). *Summary Information on Whale Shark and Cetacean Interactions in the Tropical WCPFC Purse Seine Fishery*. SCIENTIFIC COMMITTEE EIGHTH REGULAR SESSION. [Online]. Busan, Republic of Korea: Western and Central Pacific Fisheries Commission. Available at: <http://www.spc.int/oceanfish/>. [Accessed: 9 June 2017].
- St Helena Government (2015). *State of the Island*. [Online]. Jamestown, St Helena: St Helena Government. Available at: <http://www.sainthelena.gov.sh/wp-content/uploads/2013/01/State-of-the-Island-2015.pdf>. [Accessed: 15 June 2017].
- St Helena Government (2016). *ENVIRONMENTAL PROTECTION ORDINANCE 2016*. Jamestown, St Helena: Environmental Management Division.
- Stacey, N., Karam, J., Meekan, M., Pickering, S., and Ninef, J. (2012). Prospects for whale shark conservation in Eastern Indonesia through bajo traditional ecological knowledge and community-based monitoring. *Conservation and Society*, 10(1), 63. Available at: [Accessed: 4 June 2017].
- Stevens, J. (2007). Whale shark (*Rhincodon typus*) biology and ecology: A review of the primary literature. *Fisheries Research*, 84(1), 4-9. Available at: [Accessed: 5 February 2017].
- Stewart, B. and Wilson, S. (2005). Threatened Fishes of the World: *Rhincodon typus* (Smith 1828) (Rhincodontidae). *Environmental Biology of Fishes*, 74(2), 184-185. Available at: [Accessed: 30 May 2017].
- Taylor, J. and Pearce, A. (1999). Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. *Journal of the Royal Society of Western Australia*, [Online]. 82(2), 57-65. Available at: [https://www.researchgate.net/publication/228772170\\_Ningaloo\\_Reef\\_currents\\_implications\\_for\\_coral\\_spawn\\_dispersal\\_zooplankton\\_and\\_whale\\_shark\\_abundance](https://www.researchgate.net/publication/228772170_Ningaloo_Reef_currents_implications_for_coral_spawn_dispersal_zooplankton_and_whale_shark_abundance). [Accessed: 2 June 2017].
- Taylor, G. (1994). *Whale sharks*. 1st edn. New York: Angus & Robertson.
- Taylor, J. (2007). Ram filter-feeding and nocturnal feeding of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Fisheries Research*, 84(1), 65-70. Available at: [Accessed: 21 April 2017].

- Theberge, M. and Dearden, P. (2006). Detecting a decline in whale shark *Rhincodon typus* sightings in the Andaman Sea, Thailand, using ecotourist operator-collected data. *Oryx*, 40(03), 337. Available at: [Accessed: 9 June 2017].
- Thums, M., Meekan, M., Stevens, J., Wilson, S., and Polovina, J. (2012). Evidence for behavioural thermoregulation by the world's largest fish. *Journal of The Royal Society Interface*, 10(78), 20120477-20120477. Available at: [Accessed: 3 June 2017].
- Topelko, K. and Dearden, P. (2005). The Shark Watching Industry and its Potential Contribution to Shark Conservation. *Journal of Ecotourism*, 4(2), 108-128. Available at: [Accessed: 22 May 2017].
- Trujillo-Córdova, J., Cárdenas-Palomo, N., Mimila-Herrera, E., and Reyes-Mendoza, O. (2016). Whale shark behavior with swimmers and boats present during tourism activities in the northern Mexican Caribbean. *QScience Proceedings (The 4th International Whale Shark Conference)*, [Online]. Available at: <http://www.qscience.com/doi/pdf/10.5339/qproc.2016.iwsc4.63>. [Accessed: 1 June 2017].
- Van Tienhoven, A., Den Hartog, J., Reijns, R., and Peddemors, V. (2007). A computer-aided program for pattern-matching of natural marks on the spotted raggedtooth shark *Carcharias taurus*. *Journal of Applied Ecology*, 44(2), 273-280. Available at: [Accessed: 5 April 2017].
- Wang, Y., Li, W., Zeng, X., and Cui, Y. (2012). A short note on the horizontal and vertical movements of a whale shark, *Rhincodon typus*, tracked by satellite telemetry in the South China Sea. *Integrative Zoology*, 7(1), 94-98. Available at: [Accessed: 7 May 2017].
- Webb, D., Clingham, E., Collier, A., Stoll, T., and Dove, D. (2016). Improving laser-photogrammetry precision for estimates of whale shark total length and applying them to a previously unstudied aggregation of whale sharks at St. Helena Island. *QScience Proceedings (The 4th International Whale Shark Conference)*, [Online]. Available at: <http://www.qscience.com/toc/qproc/2016/2>. [Accessed: 3 March 2017].
- White, W. and Cavanagh, R. (2007). Whale shark landings in Indonesian artisanal shark and ray fisheries. *Fisheries Research*, 84(1), 128-131. Available at: [Accessed: 4 June 2017].
- Wilga, C., Hueter, R., Wainwright, P., and Motta, P. (2001). Evolution of Upper Jaw Protrusion Mechanisms in Elasmobranchs. *American Zoologist*, 41(6), 1248-1257.
- Wilson, S. (2002). A whale shark feeding in association with a school of giant herring at Ningaloo Reef, Western Australia. *Journal of the Royal Society of Western Australia*, [Online]. 85, 43-44. Available at: [http://www.rswa.org.au/publications/Journal/85\(1\)/wilson85\(1\).pdf](http://www.rswa.org.au/publications/Journal/85(1)/wilson85(1).pdf). [Accessed: 24 May 2017].
- Wilson, S. and Martin, R. (2003). Body markings of the whale shark: vestigial or functional?. *Western Australian Naturalist*, [Online]. 118-134. Available at: [http://elasmoresearch.org/publications/pdfs/whale\\_shark\\_pigmentation.pdf](http://elasmoresearch.org/publications/pdfs/whale_shark_pigmentation.pdf). [Accessed: 28 May 2017].
- Wilson, S., Polovina, J., Stewart, B., and Meekan, M. (2005). Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology*, 148(5), 1157-1166. Available at: [Accessed: 5 June 2017].

- Wilson, S., Stewart, B., Polovina, J., Meekan, M., Stevens, J., and Galuardi, B. (2007). Accuracy and precision of archival tag data: a multiple-tagging study conducted on a whale shark (*Rhincodon typus*) in the Indian Ocean. *Fisheries Oceanography*, 16(6), 547-554. Available at: [Accessed: 1 June 2017].
- Wilson, S., Taylor, J., and Pearce, A. (2001). The Seasonal Aggregation of Whale Sharks at Ningaloo Reef, Western Australia: Currents, Migrations and the El Niño/ Southern Oscillation. *Environmental Biology of Fishes*, 61(1), 1-11. Available at: [Accessed: 26 May 2017].
- Wolfson, F. and Notarbartolo-di-Sciara, G. (1981). Whale Shark Bibliography. *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, [Online]. 122(3-4), 171-203. Available at: <http://escholarship.org/uc/item/4xd5r8q6>. [Accessed: 4 March 2017].
- Womersley, F., Leblond, S., and Rowat, D. (2016). Scarring instance and healing capabilities of whale sharks and possible implications. *QScience Proceedings (The 4th International Whale Shark Conference)*, [Online]. Available at: <http://www.qscience.com/toc/qproc/2016/2>. [Accessed: 5 June 2017].