University of South Wales
Prifysgol De Cymru

Analysis of the Phoretic Relationship Between Whale Sharks (*Rhincodon typus)* and Remora (*Remora remora*) in the South Ari Atoll Marine Protected Area of the Maldives, as a Non-Invasive Associative Method for Classifying Levels of Recuperation in Sharks Following Deep Dives.

A Dissertation submitted to the University of South Wales as part fulfilment of BSc Natural History.

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Abstract

Whale sharks partake in deep dives to feed on plankton during diurnal migration. As whale sharks are ectotherms, these deep dives where colder, oxygen depleted waters are experienced affect the metabolism, cognitive ability and physiological aspects such as muscular function in this species.

Such deep dives are often followed by prolonged surface swims in a pattern of behaviour known as oscillatory vertical displacement. It is widely theorised that these surface intervals are a form of thermoregulation behaviour in an attempt to recuperate from the physiological limitations experienced as a result of deep dives. It is therefore assumed that the longer a shark has spent in warmer surface waters, the more active it will be due to greater recuperation time and thus, improved muscular and cognitive ability.

Whale sharks are found year round in the South Ari Atoll Marine Protected Area (S.A.MPA) of the Maldives, where they play host to remoras; it has been noted that remoras are almost always found attached to more active sharks.

This study statistically analyses the association between remora attachment and whale shark behaviour of those individuals frequenting the S.A.MPA, in an attempt to establish whether remora attachment can be used as an associative method for classifying recuperation levels in whale sharks.

Surveys were conducted for a period of one month in collaboration with the Maldives Whale Shark Research Programme (MWSRP) during the wet, southwest monsoon season. The data collected in situ, along with a historical data set of 2661 encounters was used in the statistical analysis of this study.

The significance of association between remora attachment and whale shark behaviour was statistically tested, as well as the influence of morphological, environmental and anthropogenic variables on both shark behaviour and remora attachment likelihood.

Results from the study revealed a significant association between active sharks and remora attachment, yet also highlighted the importance of alternative determinants in both whale shark behaviour and remora attachment likelihood.

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1. Introduction

1.1. A Review of the Biology and Ecology of the Whale Shark (*Rhincodon typus*)

1.1.1. Classification & Conservation Status

Whale sharks *(Rhincodon typus*) belong to the monotypic family Rhincodontidae within the order Orectolobiformes which consists of 42 species including, leopard sharks (*Stegstomidae*), nurse sharks (*Ginglymostoma cirratum*) and wobbegongs (*Oretolobidae*: Rowat and Brooks, 2012).

In November, 1999 the whale shark was added to Appendix II of the Bonn Convention of Migratory Species (CMS, 1999) as, "A species whose conservation status would benefit from the implementation of international co-operative agreements". In 2000, the species was listed as "Vulnerable" by the International Union for Conservation of Nature (IUCN, 2000) due to its declining population as a result of harpoon fisheries, incidental capture, and harvesting of aquatic resources. This designation was followed by legal protection in many nations including the Maldives (Fowler, 2000; Norman, 2004). In November 2002, the whale shark was additionally listed on Appendix II of the Convention on the International Trade in Endangered Species (CITES, 2002).

1.1.2. Distribution

Unlike any other Orectoloboid, the whale shark is fundamentally pelagic (Rowat and Brooks, 2001), with the first scientific description of the species recorded in the Western Indian Ocean (Smith, 1828). Despite the natural histories of many pelagic migrants having been described, knowledge and understanding of the biology, ecology and behaviour of this shark is very limited; scientific literature is predominantly restricted to locality records (Gunn, 1999). Up until 1985 there were approximately only 320 confirmed sightings of this animal (Wolfson, 1986). Today, greater numbers are observed due to increased observational effort (Beckley *et al.*, 1997; Rowat *et al.*, 2009; Speed *et al.*, 2009; Riley *et al.*, 2010).

It is known that this shark is a highly mobile species, spending large portions of its life in the open ocean and is habitually solitary (Compagno, 1984). However, groups have been recorded in association with seasonal plankton blooms and mass coral spawnings that occur off Ningaloo Reef in Western Australia (Rowat, 2010), snapper spawnings at Gladden Spit in Belize and red crab spawning at Christmas Island (Simpson, 1991; Gittings *et al.*, 1992; Taylor, 1994).

Deeming this species as "migratory" is somewhat debatable; migration denotes movement from one area to another in a predictable fashion. As this species' priorities in life change due to factors such as sexual maturity the only true migration is to predictable seasonal feeding opportunities (J. Hancock. *pers. comm.*, 2016). They are therefore regarded as a broad ranging species and are found globally in many areas with surface sea water temperatures of 18–30ºC (Fowler, 2000). Thus, this shark is a cosmopolitan tropical and warm temperate species, with its spatial distribution consisting of both oceanic and coastal environments between 30ºN and 35ºS, occurring in many Indian Ocean states including the Maldives (Figure 1; Compagno, 2001).

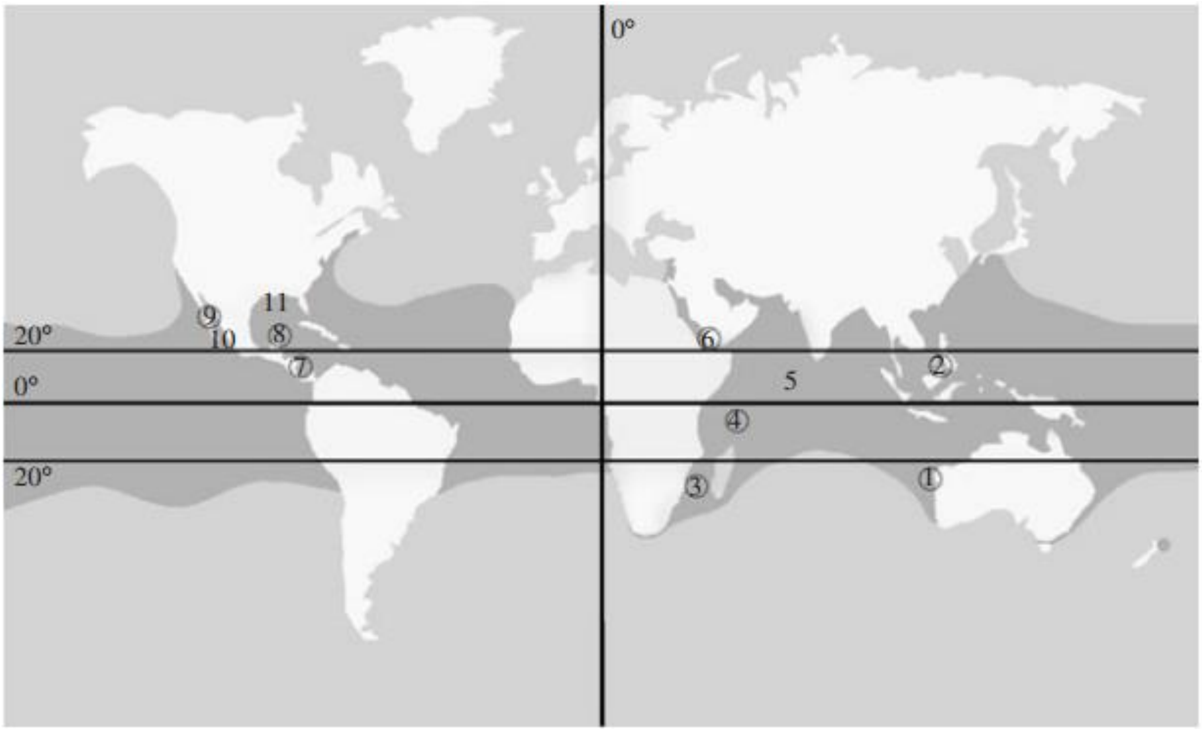

Figure 1. Global range of whale shark distribution with current known aggregation areas: 1, Ningaloo; 2, Philippines; 3, Mozambique; 4, Seychelles; 5, Maldives; 6, Djibouti; 7, Belize; 8, Holbox; 9, North Gulf of California; 10, South Gulf of California; 11, North Gulf of Mexico (reproduced from Rowat and Brooks, 2012).

Although the broader scale movement patterns and behaviours are unknown, the recorded population structure comprises a sex bias of 81% males. This suggests that these fish constitute a sub-set of the entire population (Brunnschweller *et al.*, 2009). The majority of coastal aggregations of whale sharks are dominated by immature males of around 5-7m in length (Heyman *et al.*, 2001; Meekan *et al.*, 2006).

1.1.3. Morphology

This species is one of only ten sharks that routinely attain lengths over four metres, and is the largest extant chondrichthyan (Taylor *et al.*, 1983; Compagno, 2001; Freedman and Noakes, 2002). The largest reported individual to date was recorded at 20m in total length and had a mass of 34 tonnes (Chen *et al.*, 1997); like most sharks, the females are larger than males.

Whale sharks have a moderately stout, fusiform body, with three prominent longitudinal ridges, termed “carnia”, on its upper flanks extending from near the gill region, (which encompasses a vestigial first gill known as a spiracle just behind the eye) to the caudal peduncle (Rowat and Brooks, 2012). It possesses a semi-lunate caudal fin and rudimentary barbels on the nostrils. Its skin is up to 14cm thick (Compagno, 1973) comprised of dermal denticles which are hydrodynamic in form, reducing drag and surface noise production (Figure 2: Bigelow and Schroeder, 1948).

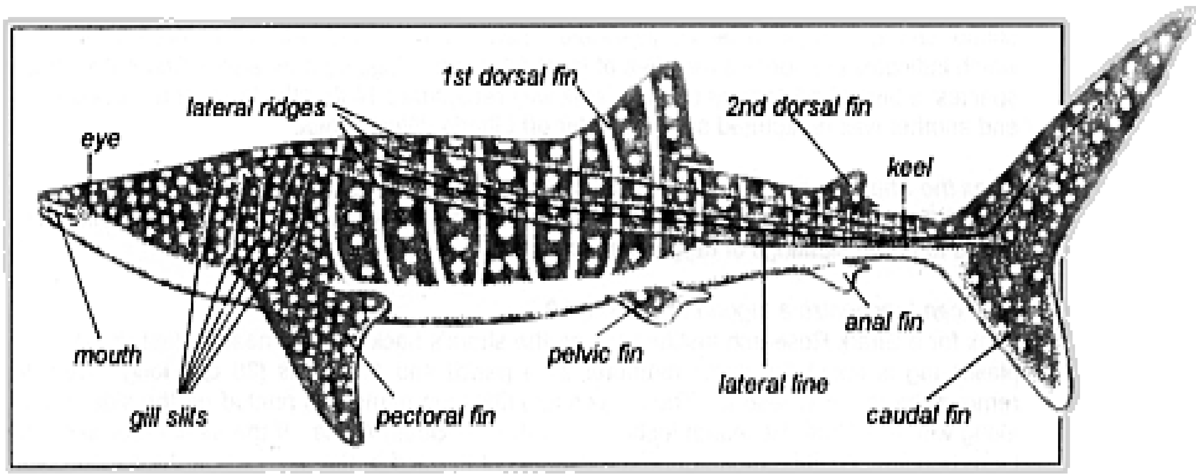

Figure 2: Morphological features of a whale shark (Florida Museum of Natural History).

The head is broad, dorso-ventrally flattened, with a large and almost terminal transverse mouth reaching up to a possible 1.5 metres in width. The mouth contains around 3000 teeth aligned in 300 rows covered by a velum of skin. However, the teeth are somewhat redundant and not utilised in feeding. Instead these sharks use gill rakers as a mechanism for separating prey from the vast volumes of water they filter (Hennemann, 2001). These cartilaginous processes which project from the brachial arch clean the captured prey from the gills as the shark closes its pharynx and ejects the water through said gills (Heyman *et al*., 2001).

The ventral surface of the body is white and each shark has a unique pattern of spots which sometimes coalesce to form short stripes on both the dorsal and lateral surfaces; these patterns serve as a finger print and are therefore considered an accurate method for identifying individuals (Norman, 2006). This method is based on two assumptions:

- Patterns do not change with age; and
- Each shark truly does have a unique spot pattern.

These characteristic body markings are a combination of two forms of camouflage; spots and stripes being disruptive colouration, while the lighter ventral surface is deemed counter shading (Figure 3: Wilson and Martin, 2003). This method of identification has been widely applied to a number of species allowing biologists to address critical conservation-based questions regarding demography, reproduction and dispersal of rare and endangered species including: mountain lions (*Felis concolor)*; marbled salamander (*Ambystoma opacum)* and badgers (*Musteloidea*: Pennycuick, 1970; Grigione, 1999; Dixon, 2003; Gamble *et al.,* 2007).

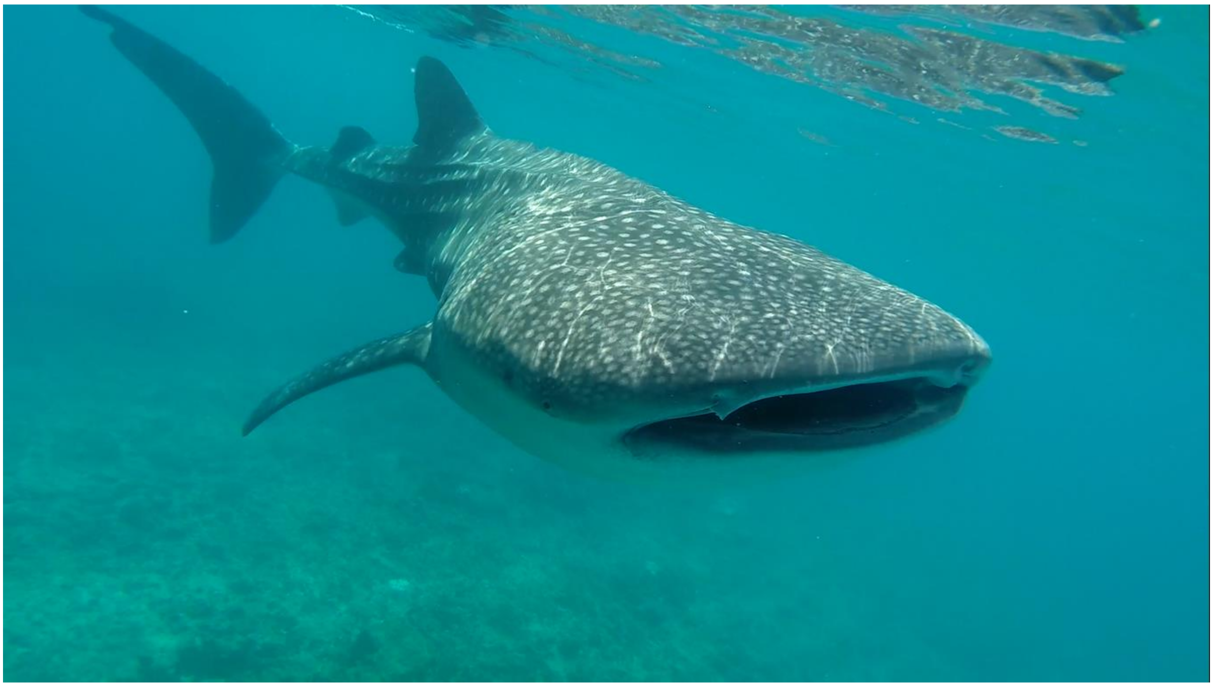

Figure 3. A juvenile male shark. Note the carnia, fusiform mouth and contrasting colouration (Photograph provided by Victoria Haid, 2015).

1.1.4. Life History

This shark's life history is poorly understood; its longevity is uncertain, but may be as much as 100 years (Compagno, 2001). Sexual maturity is thought to occur at approximately 30 years of age, at suggested lengths of 8m for males and approximately 9m for females (Norman and Stevens, 2007). Only one pregnant female has ever been recorded; in 1995 a 10.6m female was captured off the coast of Taiwan with 304 embryos of which 237 were sexed (Joung *et al.*, 1996). Of these, 114 were male and 123 female indicating a 50:50 sex ratio (Joung *et al.*, 1996; Leu *et al.*, 1997). The embryos consisted of three maturity classes within a twin uteri, some already having hatched from their eggs with a body length of approximately 70cm. Thus, whale sharks were deemed ovoviviparous and the most fecund of all K-selected sharks (Rowat, 2010). Genetic analysis of 29 of the pups indicated a single paternity (Schmidt *et al.*, 2010) providing strong evidence for monoandry (Rowat and Brooks, 2012).

1.1.5. Diet

Whale sharks are planktivores, feeding on dense aggregations of euphausiid, copepods, fish eggs and occasionally mobile prey such as small fish. This species is capable of filtering over 6000 litres of water an hour (Hennemann, 2001) and primarily engages in energetically expensive methods to gather food because of the enormous increase in hydrodynamic drag when they feed (Sims, 1999; Goldbogen *et al.*, 2007).

Despite being slow swimmers at speeds of no more than 5km/h, they can dive to extreme depths; certainly more than 1900m (Compagno, 2001). A study on the diving behaviours of whale sharks in the Red Sea provides evidence that this species may rely at least to some degree on prey items, such as plankton, from depths below the euphotic zone- the uppermost 80m of the ocean surface (Graham, 2006; Rowat 2007; Rohner 2013). Long, slow gliding descents and continuous ram ventilation (the act by which a shark swims forward whilst the mouth is continuously open, allowing water and suspended food to be filtered into the gills) is performed to reach this plankton during diurnal migration in relatively cold waters, up to 20°C cooler than the surface; such descents could rapidly cool bodily tissues and circulating blood (Berger *et al.,* 2015). It must be remembered that whale sharks are ectothermic animals. It is known in many ectotherms, though never specifically proven in whale sharks, that low body temperatures affect metabolism, cognitive ability and physiological aspects such as muscular function (J. Hancock. *pers. comm*., 2015). These sharks are therefore able to access deeper habitats; whilst the bulk of their bodies reduces surface area and thus preserves heat, physiological limitations may be experienced and recent studies have shown this has metabolic consequences for these ectotherms (Thums *et al.*, 2013). Hence the need for post deep dive thermoregulatory and physiological recuperation behaviours.

1.1.6. Thermoregulatory Behaviour and Physiological Recuperation

Oscillatory vertical displacement is a pattern of regular movement between the surface, or near-surface, and deep waters. It describes deep dives followed by prolonged surface swims, a behaviour recorded in coastal transient sharks, such as whale sharks (Gunn *et al.,* 1999, Wilson *et al.*, 2006). Several tagging studies, including one done by the Maldives Whale Sharks Research Programme (MWSRP) in 2008/09, show that whale sharks follow a regular profile of diving and then ascending to near the surface (R. Rees. *pers. comm.*, 2015).

It has been suggested that plankton use these areas of greater depth for protection against predation and this results in what is known as the diurnal migration (Roberts, 2007). Sharks diving to these meso- and bathypelagic depths may be indicative of foraging behaviour, following the diurnal course of their diet (Rowat and Brooks, 2012).

The minimum temperatures experienced by sharks on these deep dives are inversely related to the time spent in surface waters following ascent, suggesting that whale sharks swim at the surface as a form of behavioural thermoregulation allowing them to warm up after losing heat at greater depths (Thums *et al*., 2013); this affinity for the surface is thought to be related to the recovery of body heat lost at depth. This hypothesis of thermal recovery is one of the most widely cited to explain this phenomenon (Klimley, 2002). It suggests that surface intervals after diving are required to return the body temperature to levels necessary to regulate physiological processes after time spent in cooler, deeper waters and is one of the few hypotheses explaining differential use of the surface and deep habitats with empirical support (Gunn *et al.,* 1999; Graham *et al.*, 2006; Shepard *et al.,* 2006; Campana *et al.*, 2011 Thums *et al.,* 2012).

Aside from cold temperatures, another factor a deep diving fish has to contend with is the Oxygen Minimum Zone (OMZ). This is a layer of ocean typically 200-1000m down which has the least amount of oxygen saturation, and thus redox conditions (the level of oxidation reduction) are hypoxic (O_2 concentration <75 μmol/L) or anoxic (O_2 concentration <1 μmol/L; Kamykowski, 1990).

The MWSRP have noted that whale shark sightings tend to peak at periods of strongest tidal flows along the reefs of the South Ari Atoll Marine Protected Area (S.A.MPA) of the Maldives and observed, though not significantly shown, that the shark's direction of travel is often headlong into the current flow. It may be that if a shark was oxygen depleted, swimming headlong into a strong current flow could reduce the amount of energy required to pass water over the gills during recuperation. Thus, the behaviour of a shark could reflect its level of recuperation. For example, a shark which has nearly reached an optimal body temperature and level of oxygenation, would have improved muscular and cognitive function, and so be more likely to exhibit active behaviours such as feeding, swimming rapidly or showing curiosity.

1.2. Whale Sharks in the Maldives

1.2.1 Impacts of Eco-Tourism

Due to the whale sharks' low abundance, K-selected life history, highly nomadic nature, and value in international trade, it is significantly vulnerable to commercial fishing (IUCN, 2000). Dive and snorkel-based marine eco-tourism has grown significantly in recent years, with this species being one of the main attractions in multiple locations, including Australia, the Philippines, Belize and the Maldives. Consequently, the sharks in these areas are subject to high levels of recreational marine-based activities, increasing threats of collision with vessels and disturbance to their natural behaviour by unregulated tourism. However, this lucrative industry has demonstrated the worth of this fish to be far greater alive than dead which has subsequently led to conservation initiatives for this animal.

1.2.2 The Maldives Whale Shark Research Programme (MWSRP)

The Maldives Whale Shark Research Programme (MWSRP), is a research-based conservation charity dedicated to studying whale sharks through citizen science data collection, and fosters community-focused conservation initiatives in the Maldives and the greater Indian Ocean. The charity’s research is conducted within the South Ari Atoll Marine Protected Area (S.A.MPA; Figure 6) of the Maldives. Its primary focus is to advance knowledge of this species and advocate conservation policies; in 2009, the programme’s work on the core habitats of this species helped provide the baseline data needed for the creation of the S.A.MPA.

Founded in 2006 by James Hancock and Richard Rees, it initially began as a scientific expedition which has since grown into the only long term organisation dedicated to researching whale sharks within the Maldives; it became a formally registered charity in the UK in 2008, and in the Maldives in 2013.

To date, the charity has 265 identified sharks within its database, based on the identification of a shark using its unique spot patterns as a fingerprint. The research has shown that the whale sharks which frequent the S.A.MPA are almost exclusively adolescent sharks, with an average size of 5.92m. There is also a strong male sex bias in the population, with just 9% of the 265 recorded sharks to date being female (MWSRP, 2016); this biased ratio is homogenous throughout all recorded whale shark population dynamics.

1.2.3 Whale Sharks in the South Ari Atoll Marine Protected Area (S.A.MPA)

A 6 year study by Riley *et al.,* (2010) recorded regular re-sightings at the southern fringe of the S.A.MPA, supporting the hypothesis of local site fidelity of these sharks during some period of their lives. These observations suggest that a large number of the sharks that are observed in the S.A.MPA may be site-faithful or perhaps permanent residents of the archipelago, at least until sexual maturity. One reason for these distorted ratios and size characteristics of aggregations may be that only smaller male sharks approach close enough to the reefs on which they can be observed (Riley *et al.,* 2010). Thus, females are under-represented in the current data leading to distorted ratios. There is some evidence to suggest that females may occupy a distinct and more pelagic habitat compared to males (Borrell *et al.,* 2011). However, exactly when this change in habitat use occurs in not known.

It is theorised that the S.A.MPA, with its ambient warmth and the highly oxygenated waters, is utilised by the sharks in an effort to manage recuperation following deep dives up to 1600m with temperatures of 3ºC and very low oxygen levels (Hennemann, 2001). Additionally, it is thought that perhaps the shallow fore reef, with a maximum depth of 20m, offers protection for these sharks which are predominantly juvenile (J. Hancock. *pers. comm.,* 2015); there have been reports of attacks on infant whale sharks by blue marlins (*Makaira nigricans*) and blue sharks (*Prionace glauca*: Kukeyev, 1996).

1.3. A Review of the Biology and Ecology of the Remora (*Echeneidae*)

1.3.1. Life History

Remoras are a Carangoid fish, belonging to the Echeneidae family which spend their adult life as commensals on large pelagic vertebrates. The first recorded report of an association between remora species and whale sharks was in 1883; several remora were discovered residing in the mouth of a shark (Chierchia, 1884). The relationship between remoras and their host is generally thought to be a phoretic one. The host's role as a vehicle is obvious and as such the rider is passively transported reducing energy expenditure, provided with a respiratory flow of water (Strasburg, 1957) and provision of food in the form of ectoparasites or scraps (Strasburg, 1959); remora are opportunistic feeders of plankton, ectoparasites and shedding skin of their symbiont. Based on observation of this species in captivity, remora require a swift passage of water over the gills to survive and can thus not reside in still waters (Bohlke and Chaplin, 1993).

1.3.2. Morphology

The dorsal fin has undergone dramatic evolutionary transformation, modifying it into a large segmented suction disk allowing adhesion to the host species (Figure 4: Santini *et al.*, 2014). The disk is made of serial parallel pectinated lamellae which are homologous to the dorsal fin elements of other fishes. Small tooth-like projections of mineralized tissue from the dorsal pad lamella, known as spinules, are thought to increase the remora's resistance to slippage thereby enhancing friction to maintain attachment to a moving host (Beckert *et al.*, 2015).

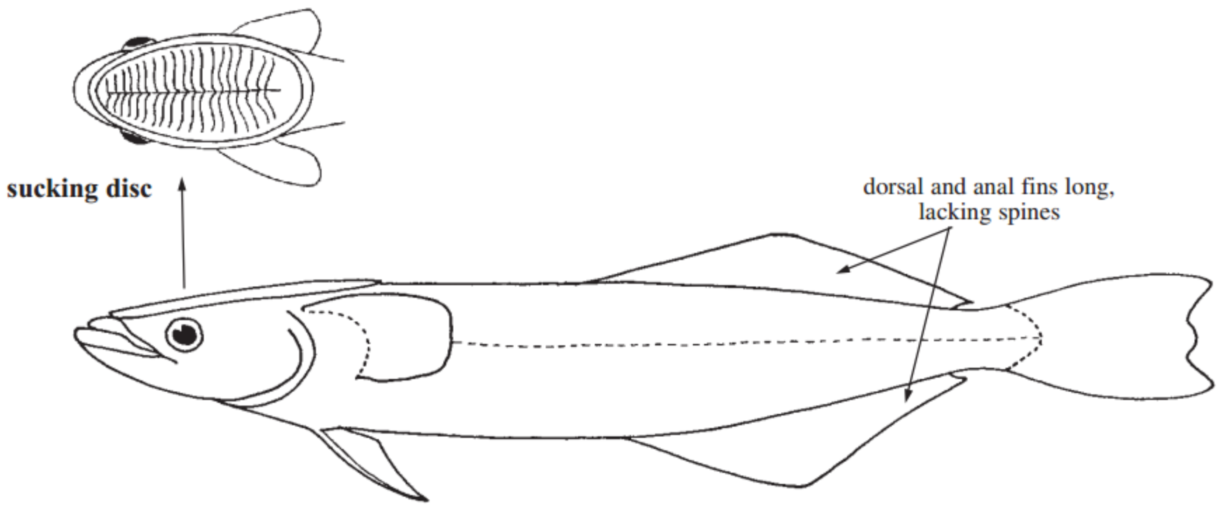

Figure 4. The remora and its suction disk (Linnaeus, 1758).

1.3.3. Attachment and Host Fidelity

Strasburg (1962) found that a remora's urge to attach is equally important as that to feed; despite this species' ability to detect food at least 38cm laterally and 122cm ventrally, remoras will abandon food within a distance of >30cm to reattach to their host. In addition, it was found that following detachment each remora returned to precisely the same location on its original host, orientating itself to the exact shape and position previously held. Considering this species has little to no dorso-vision, this re-positioning is thought to be achieved through another sense. The texture of the host's skin is altered through extended periods of contact with the suction disk. Therefore, reattachment is deemed tactile, and this altered surface area enables the remora to re-establish itself in the same location via touch. This study alludes to the notion that remora attachment is sustained once established and suggests some measure of host fidelity. Although difficult to recognise, remora host fidelity has been documented in the wild. It is hypothesised that this fidelity serves as a reproductive strategy, increasing the chance of mating opportunity as the host facilitates encounters between potential mating partners. Martins and Ivan (2003) indicate that this behaviour is not uncommon amongst members of the Echeneidae family.

1.3.4. Remora in the South Ari Atoll Marine Protected Area.

The most regularly encountered species of remora in the S.A.MPA, is *Remora remora*, which is recorded at depths of 0-200m (Fricke *et al.*, 2011). MWSRP have observed, that remora are almost always found attached to more active, and therefore theoretically more fully recuperated sharks (Figure 5: J. Hancock. *pers. comm*., 2015)**.** It has subsequently been theorised that this is due to the prolonged surface interval time resulting in a greater period of opportunity for remora to attach. In addition to this, the observation of remora being attached predominantly to active sharks in the S.A.MPA may be a reflection of the remora's need for this swift passage of water over the gills, which can be better provided by more active sharks and thus, shark behaviour may be a factor in remora host preference.

Figure 5. Remora attaching to a whale shark in the S.A.MPA. (MWSRP, 2013/14).

2. Study Aims and Objectives

The aim of this study is to investigate whether the presence or absence of remora attached to a whale shark can be used as a non-invasive and associative method for classifying the level of recuperation of any given individual shark. If results show any statistical significance this may contribute to the practice of monitoring sharks in this region, acting as a precursor for more in depth research into this association as a method for determining a whale shark’s level of recuperation. Additionally, this may provide further evidence to the importance of this area as a vital habitat used for the recuperation of these animals following deep dives, necessary for the efficient functioning of these sharks’ metabolic processes, and may subsequently aid in further government protection.

Three research hypotheses are proposed as theoretical assumptions for the association between remora attachment, whale shark behaviour and the subsequently indicated level of recuperation. These are:

- A lethargic shark’s direction of travel is headlong into the current to reduce the amount of energy required to pass water over the gills during recuperation from deep dives;
- The presence of remora on a shark indicates prolonged surface time and so presumed increase in body temperature and oxygen levels, characterised through behaviour classed as active (feeding, fast swimming, or inquisitive); and
- The absence of remora indicates a shark recently entering shallow water from below 100m, presumably with lower body temperatures and oxygen levels, characterised by lethargic behaviour (cruising, passively evasive).

In order to test these hypotheses, the study will assess the significance of associations between whale shark behaviour and direction of travel, and whale shark behaviour and remora attachment. Additionally, morphological, environmental and anthropogenic variables are considered as potential determinants for remora attachment. These are statistically analysed for significance in an attempt to determine whether they have a confounding influence on remora attachment. To achieve this there are a number of supporting objectives:

1) Determine if shark size influences the likelihood of remora attachment;

2) Determine if sea state, season and sea surface temperature influence both whale shark behaviour and likelihood of remora attachment; and

3) Determine if the number of boats and persons present during whale shark encounters influence both whale shark behaviour and remora attachment likelihood.

3. Method

3.1. The Study Site

The South Ari Atoll Marine Protected Area (S.A.MPA) of the Maldives is an important habitat for the whale shark and is one of few places globally where it is known whale sharks, locally named “Fehurihi”, inhabit all year round (Hennemann, 2001). The S.A.MPA is characterised by warm waters maintained at 27-32˚C throughout the year. It experiences two seasons: the dry northeast monsoon from November through to April; followed by the wet southwest monsoon occurring between May and October (I. Shamyl. *pers. comm.*, 2015). It is an area unlike most other whale shark hotspots where sightings are restricted to seasons that coincide with feeding opportunities, making the S.A.MPA an ideal study site, as chances of encounters can be considered relatively high year-round.

Officially declared a protected area on the 5th June 2009, the S.A.MPA is a 42km stretch of reef and the largest marine protected area in the Maldives (Figure 6). It encompasses the region starting from the north western tip of the reef crest at Rangali Island up to the north eastern tip of Dhigurah Island (Figure 7). Its boundary extends 1km seaward from the epipelagic reef fringe and this region is commonly referred to as the Maamigilli-Dhigurah Reef (03º28'N, 72º51'E). Directive points for this region (EPA, 2010) can be found in Appendix 1.

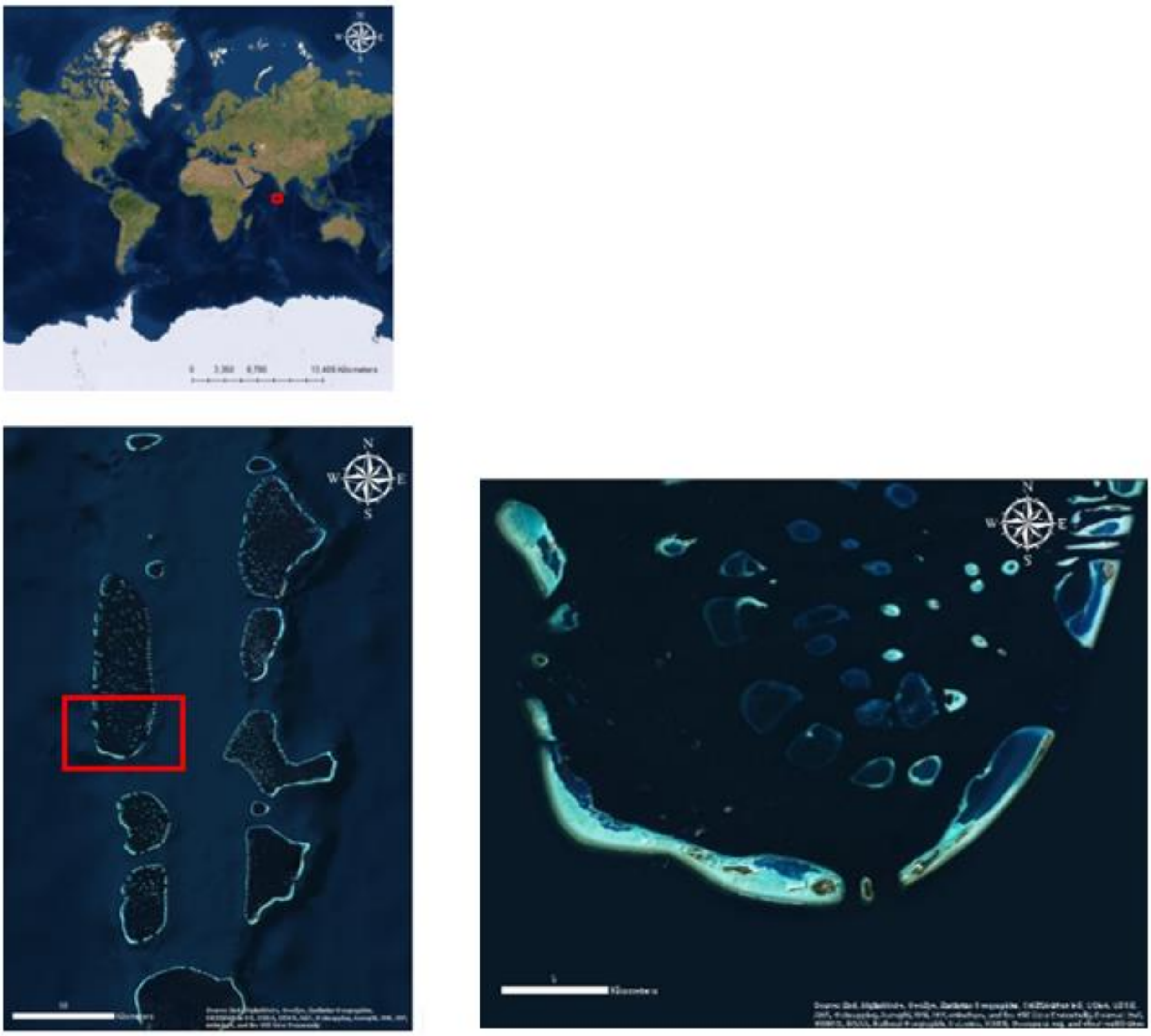

Figure 6. Map of the S.A.MPA in relation to its greater geographical surroundings.

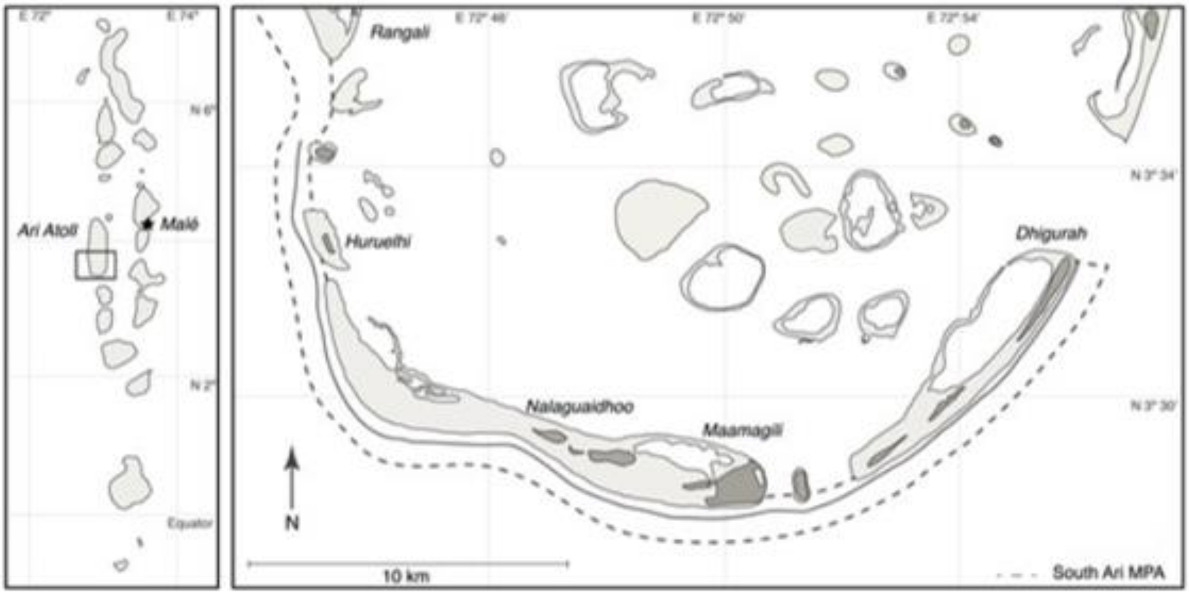

Figure 7. Diagram of the South Ari Atoll Marine Protected Area (Cagua et al., 2014).

Bathymetrically, the S.A.MPA is positioned along the western edge of the Chagos-Laccadive Plateau; a region comprised of shallow atolls and sea beds between atoll chains formed by the Réunion volcanic hotspot. The S.A.MPA encompasses an area where the outer edge of this plateau is considered to be in relatively close proximity with the deeper ocean (Figure 8).

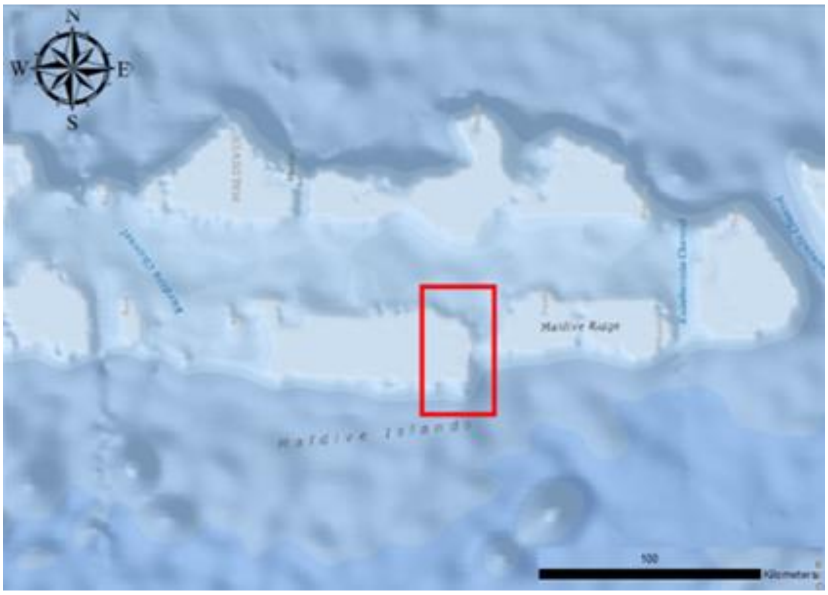

Figure 8. Bathymetric map of the Maldives, with the red box indicating the S.A.MPA.

The atoll chains along this plateau are the remains of the reefs which once surrounded volcanic islands, formed as a product of geological activity of the India and Arabian Peninsula tectonic plates in the Indian Ocean (Berghella, 2013). These volcanic islands would then begin to subside at a rate equal to the growth of the coral, subsequently leaving behind fringing reefs; with time and the further submergence of the islands peak, these fringing reefs would later develop into barrier reefs and eventually become atolls (Garrison, 2013). The ability of atolls to form in this region is due to the shallow warm, mineral rich waters required for the growth of the coral inhabiting these areas (Taylor, 2002). The lagoons inside of the atolls are a breeding ground for plankton and these microscopic organisms flow out of the lagoons into the open ocean via a kandu (Masters, 2009), thus providing a rich source of the whale sharks' diet.

3.2. Data Collection

Working alongside the MWSRP and its volunteers, data were collected using observational non-invasive adaptive surveying techniques from aboard a Dhoni (a traditional Maldivian small wooden sailing boat). This method is a form of citizen science. Citizen science is research collaboration involving members of the public, whereby volunteers participate in data collection for governing bodies and this has become widely accepted as a valuable research tool. Such research has increased the scale of ecological field studies with continent-wide, centralised monitoring efforts and the production of large, longitudinal data sets (Bonter & Cooper, 2010; Dickson *et al.,* 2010).

Surveys were conducted over a period of 20 days during the wet southwest monsoon season from the 20th July to the 14th August 2015, between the hours of 9am and 4pm daily (excluding Fridays and Saturdays as these are prayer days within the Maldives).

Prior to the onset of surveying, all project volunteers were briefed regarding survey requirements to ensure their co-operation and assistance in obtaining the required information for the purpose of this study. This briefing was conducted for every intake of new volunteers.

The Dhoni departed from Dhigurah and lapped the Maamigilli-Dhigurah Reef at speeds no greater than 5 knots. Once a whale shark was spotted, or by notification of a whale shark sighting from either other vessels along the reef or from an aerial lookout, the whale shark was approached by boat to within a maximum distance of 15m at speeds of no greater than 2 knots. At this point the time, GPS co-ordinates and direction of travel by the shark (into or with the water current) were taken using an Oregon 550 GPS (Garmin). Sea state was recorded as calm, slight, moderate or rough.

Volunteers along with co-ordinators then entered the water equipped with a snorkel, mask and fins. All members would approach the shark up to a distance of 4m and participate in the recording of: remora presence and number; identifying marks on the shark such as scars or wounds; estimations of the number of persons in the water and the number of surrounding boats during the encounter, and the behaviours exhibited by the shark as described in Table 1. These behaviours are not mutually exclusive and a variety of differing behaviours, speeds and activity levels can occur within a lone encounter. All variables were recorded on a standardised encounter form that has been consistently used by MWSRP (Appendix 2 and 3).

Table 1. Description of whale shark behaviours.

Behaviour	Description
Cruising	Describes consistent, low speed swimming with no obvious reactions to surrounding stimulus or feeding behaviour.
Inquisitive	Denotes sharks which remain in one area of human activity for a prolonged time, often approaching people in the water.
Evasive	Denotes sharks that display obvious and immediate changes in swimming speed, direction or depth as an avoidance response to approaching humans-the opposite of inquisitive.
Ram Filter Feeding	Describes the act by which the animal swims forwards whilst the mouth is continuously open, allowing water and suspended food such as plankton to be filtered into the gills where the food will be trapped and subsequently swallowed.
Suction Feeding	Occurs whilst the shark is stationary and commonly more vertical in the water column. The animal repeatedly opens and closes its mouth sucking in large volumes of water which are then expelled through the gills again, trapping any food.
Swimming Style	Slow, fast and/ or banking.
Diving	Gradual, deep and/or parabola (continuous repetition of diving and ascending).
Change of Direction	Circular, gradual and/ or parabola (continuous alternation of right and left direction).
Activity Level	1 being highly passive; 2 moderately passive; 3 neither passive nor active; 4 moderately active and 5 being highly active.

Additionally, those members of the team possessing a dive watch and the ability to free dive did so to the reef bed and recorded reef depth. If the reef was too deep for this to be achieved then reef depth was visually estimated.

These tasks were performed as a group effort during an in-water encounter and then collated to ensure the full scope of the animal and surrounding activities were recorded as swimming and free diving abilities differed between members of the team.

Prior to departure individuals were selected to collect the following at every encounter;

- Photographs (GoPro) of the area between the 5th gill slit and the leading edge of the dorsal fin on both the right and left side of the shark, in order for later identification of the shark from the unique spot pattern;
- Laser measurements of the shark using a laser photogrammetry rig (Moray). Two green lasers mounted precisely 50cm apart are projected onto the lateral side of the shark in a region between the 5th gill slit and the leading edge of the dorsal fin. A camera (GoPro) mounted between the two lasers is used to capture the two markings 50cm apart; and
- Tape measurements of the shark using a 20m plastic tape (Stanley). This method was only used during encounters with minimal numbers of tourists for health and safety reasons. These two measuring techniques have high accuracy levels shown in variation by as little as 1-2%. Shark size was then classed into three equal categories: small =0.5-4m; medium= 4.1-7.5m and large= 7.6-11.5m.

An encounter ended once the shark had reached depths in which it was no longer visible, or once all team members had returned to the Dhoni of their own accord due to fatigue. At this point the time was recorded again using the Oregon 550 GPS (Garmin); the intervening duration between this time, and that recorded at the beginning of the encounter was manually calculated and constituted the total encounter time. All observations were then recorded onto the standardised encounter form (Appendix 2 and 3).

Two additional environmental variables were recorded immediately after the encounter whilst the Dhoni remained stationary at the encounter site. These were:

- Current direction using a tennis ball and GPS. The ball was dropped into the ocean and the GPS held directly over its landing position and a reading taken. The ball was then allowed to free float for a period of 2 minutes. At the end of this period the Dhoni would be re-positioned next to the new location of said ball and a second GPS reading was taken. From this data the current direction could then be establish by determining in which direction the ball had floated; and
- Sea surface temperature (˚C) was recorded using a digital thermometer (Extek) by simply placing the gauge into the water and taking a reading.

A number of these recorded variables were subject to observer variability, therefore there is potential for inaccuracies; to counter this, all recorded data were kept at a constant level of accuracy through verification by the co-ordinators of the project who assisted volunteers on every survey.

Following departure of the Dhoni at the end of the survey period, analysis of photographs and laser measurements were conducted to identify all sharks encountered that day. The laser image is loaded onto a computer where the 50cm region is translated into a number of straight line pixels. The distance between the 5th gill and the leading edge of the dorsal is similarly established in pixels. An equation which extrapolates these measurements provides overall total length.

Identification from the spot patterns was done using an algorithm, originally founded by NASA to map constellations, known as I^3S**:** Interactive Individual Identification System. It is a computer-aided photo-identification application that has been adapted to identify individual animals and relies on natural markings (Norman, 2006).

It is utilised by selecting at least 12, and up to 15 spots that make up a whale shark's unique pattern within the boundaries of the posterior of the 5th gill slit, the dorsal of the proximal end of the pectoral fin, the anterior of the line drawn dorsoventrally from the insertion point of the posterior end of the pectoral fin and ventral of the 3rd longitudinal ridge (Figure 9).

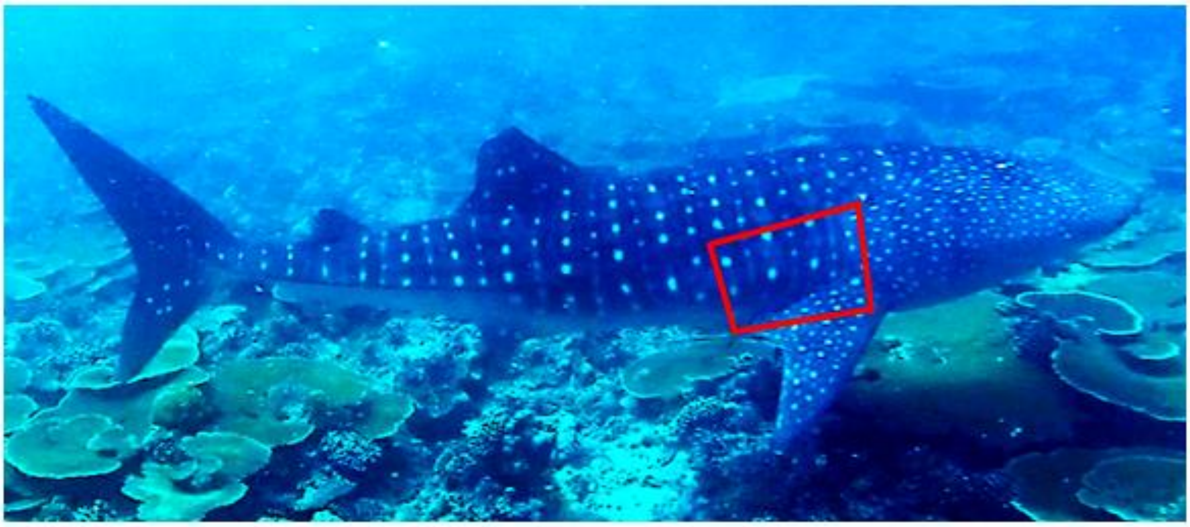

Figure 9. Representation of the use of I³S showing the area in which spots of a shark's unique pattern are to be selected for identification (Photograph by Victoria Haid, 2015).

After selection of the spots, I³S cross references the markings with all prior entries held in its accompanying database and alerts the user of a match allowing for identification of a previously seen shark; failure to find a match results in a new shark having been identified which can subsequently be named and added to the database.

A total of 25 encounters was had during the in situ data collection period. In addition to this an historical data set was obtained from director Richard Rees containing all encounters over the 10 year operating period of MWSRP. These are collated into a master excel spreadsheet for all worded information (Appendix 4) along with separate corresponding photographic evidence since the onset of the programme in 2006. This data set is inclusive of entries made by associated bodies such as the Manta Trust who report whale shark sightings to the MWSRP. In total this makes up a data set of 2661 recorded whale shark encounters for statistical analysis.

3.3. Data Analysis

The full data set of whale shark encounters from 2006-2015 was manually processed and cleaned, removing all duplicates. Each encounter was matched with its photographic record, and then allocated to one of two categories: active shark or lethargic shark. This was determined according to an ethogram devised in collaboration with MWSRP; active behaviour constituted feeding of any kind and inquisitiveness and lethargic behaviour constituted cruising or evasiveness.

If a shark was noted performing two behaviours which contradicted each other in terms of category, then the notes section of the master sheet, was used to establish the more dominant behaviour. The behaviours “diving”, and “change of direction” were excluded in the determination process as there is great potential for these behaviours to be induced by inappropriate human activity and can therefore not be considered natural occurrences. These two categories were then sub-divided into a further two categories, totaling four: active sharks with remoras; active sharks without remoras; lethargic sharks with remoras, and lethargic sharks without remoras. Allocation was done via referral to noted presence of remora for said encounter in the master excel spreadsheet; in the absence of noted remora presence, the photographic records corresponding to the encounter were studied to establish whether there were or weren’t remora present.

Due to a number of associated bodies having contributed to the historical data set, a number of encounters lacked all the mandatory variables recorded by MWSRP. For this reason, the total number of encounters used in each statistical test varies depending on the quality, accuracy and ultimately the variables being tested having been included within each encounter record.

ArcMap (GIS) was used to map the distribution of encounters using their GPS locations throughout the study area for both the 20 day period of in situ data collection (Appendix 5) and the 10 year operating period of MWSRP from 2006-2015 (Appendix 4).

IMB SPSS (PASW Statistics) was used to conduct the following statistical tests in support of the studies research hypotheses and overarching aim:

Chi^2 Tests of Independence

Chi^2 tests were conducted to investigate if there was a significant association between a shark's behaviour (active or lethargic) and its direction of travel (Appendix 6), and, if the likelihood of remora attachment was significantly different between active and lethargic sharks (Appendix 7). These tests assessed the following accompanying research hypotheses:

1. A lethargic shark's direction of travel is headlong into the current to reduce the amount of energy required to pass water over the gills during recuperation from deep dives, and may therefore be a form of recuperation behaviour.
2. Remora attachment likelihood is greater when a shark is active due to prolonged surface time and is thus, indicative of recuperation level.

Additional Chi^2 tests were performed to investigate if shark size, sea state and season significantly influenced both shark behaviour, and, remora attachment likelihood

(Appendices, 8, 9 & 10). If so this may highlight the importance of alternative variables in remora attachment likelihood and thus, question the significance of any association found between whale shark behaviour and remora attachment in relation to the theory that remora attachment is indicative of recuperation level.

Data exploration and measurement variables

Kolmogorov-Smirnov (K-S) tests were conducted to determine the distribution of the following measured variables: sea surface temperature, number of boats and persons. If a variable was found to be non-normally distributed, evidenced by a significant K-S test result, attempts were made to transform the data to a normal distribution (again tested using a K-S test of normality). The results for all three variables showed the data remained non-normally distributed ($p<0.05$) and positively skewed after appropriate data transformation. Consequently non-parametric tests were used for these variables.

Mann Whitney U Tests

Mann Whitney U test were used to establish whether the three aforementioned variables influenced both whale shark behaviour and remora attachment likelihood (Appendices, 11, 12 & 13). However, due to an insufficient number of encounters having both sea surface temperature and whale shark behaviour noted, it was not possible to conduct tests in relation to these two variables. Any statistical significance found here, would again signify the importance of external variables in remora attachment likelihood and subsequently challenge the theory that shark behaviour determines attachment, therefore attachment can be used as an associative method for classifying recuperation levels in whale sharks.

Logistic Regression

Logistic regression analysis was conducted to predict both remora attachment likelihood and whale shark behaviour using sea surface temperature, number of boats and persons as the predictors (Appendices 14, 15 & 16). These measured variables may interact in predicting the likelihood or remora attachment and the behaviour of a shark, and so the logistic regression was implemented in a step wise selection process.

Excel (Microsoft) was utilised to produce accompanying graphs and charts to provide visual representation of results.

3.4. Health and Safety

As this project was conducted aboard a vessel overseas, and involved open water swimming and free diving amongst a multitude of foreign flora and fauna, some of which are considered hazardous such as fire coral, sting rays, cone shells, scorpion fish, lion fish, stone fish, and occasionally but rarely false killer whales, a risk assessment was carried out prior to the expedition and can be found in Appendix 17.

3.5. Ethics

Strict rules were adhered to during all encounters throughout the research period to maintain an ethical approach. This includes: maintaining a minimum distance of 4m from any shark during in-water encounters; at no point making physical contact with the animal; never using flash photography, nor positioning oneself directly in front of the shark's path or swimming into its line of vision which may startle the animal. These regulations are part of a code of conduct first established by the Australian government for ecotourism at Ningaloo Reef (Department of Parks and Wildlife, 2013) and have now been adopted by ecotourism companies worldwide.

4. Results

The raw data for all encounters can be found in Appendix 4 on disc.

4.1. Whale Shark Encounters

In total approximately 63 hours of surveying was completed (7 hours daily). During this time a total of 25 whale shark encounters was made along the southern fringe of the Chagos – Laccadive Plateau within the South Ari Atoll Marine Protected Area (S.A.MPA). Of these 25 encounters, six sharks exhibited active behaviour of which none had remoras attached; the remaining 19 sharks exhibited lethargic behaviour of which two had remoras attached (Figure 10).

Figure 10. Location of the 25 sharks, their recorded behaviour and remora presence/absence. Yellow represents lethargic sharks with remora attached, red represents lethargic sharks without remora attached and pink represents active sharks without remora attached.

Over the 10 year period between 2006 and 2015, 2661 whale shark encounters have been recorded within the S.A.MPA by the Maldives Whale Shark Research Programme (MWSRP) and associate bodies, inclusive of those recorded during the 20 day in situ data collection period. Of those 2661 encounter, 625 sharks were classified as active with the remaining 2036 sharks classified as lethargic (Figure 11). Distribution of these behavioural observations within the S.A.MPA is relatively homogenous.

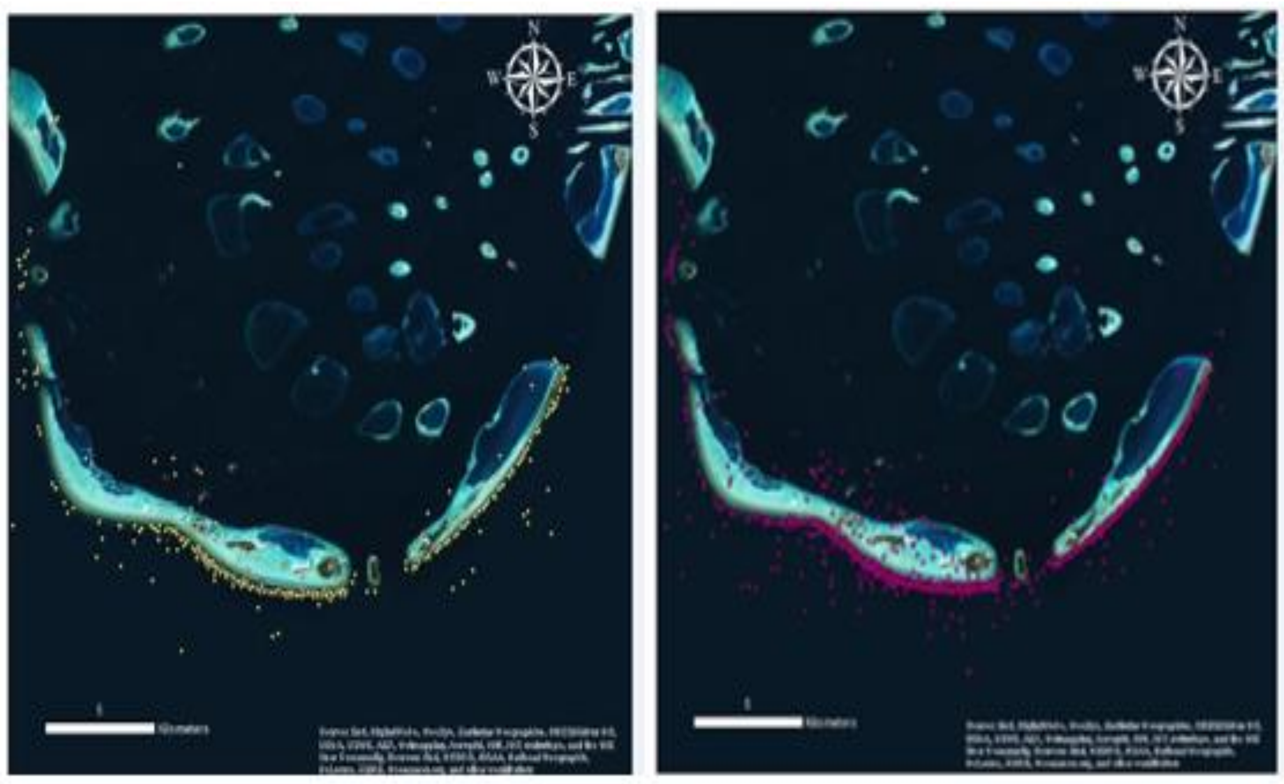

Figure 11. Locations of: lethargic sharks (left, represented in yellow), and active sharks (right, represented in pink) encountered between 2006 and 2015.

4.2. Whale Shark Behaviour and Direction of Travel

Total number of records for which both current direction and whale shark direction were recorded was 946. Of these records 26.5% (n= 251) were active sharks with the remaining 73.5% (n=695) being lethargic. Of those sharks classified as active, 45.8% (n=115) swam headlong into the current and 54.2% (n=136) swam with the current. Of those sharks classified as lethargic, 60.7% (n=422) swam headlong into the current and 39.3% (n=273) swam with the current (Figure 12).

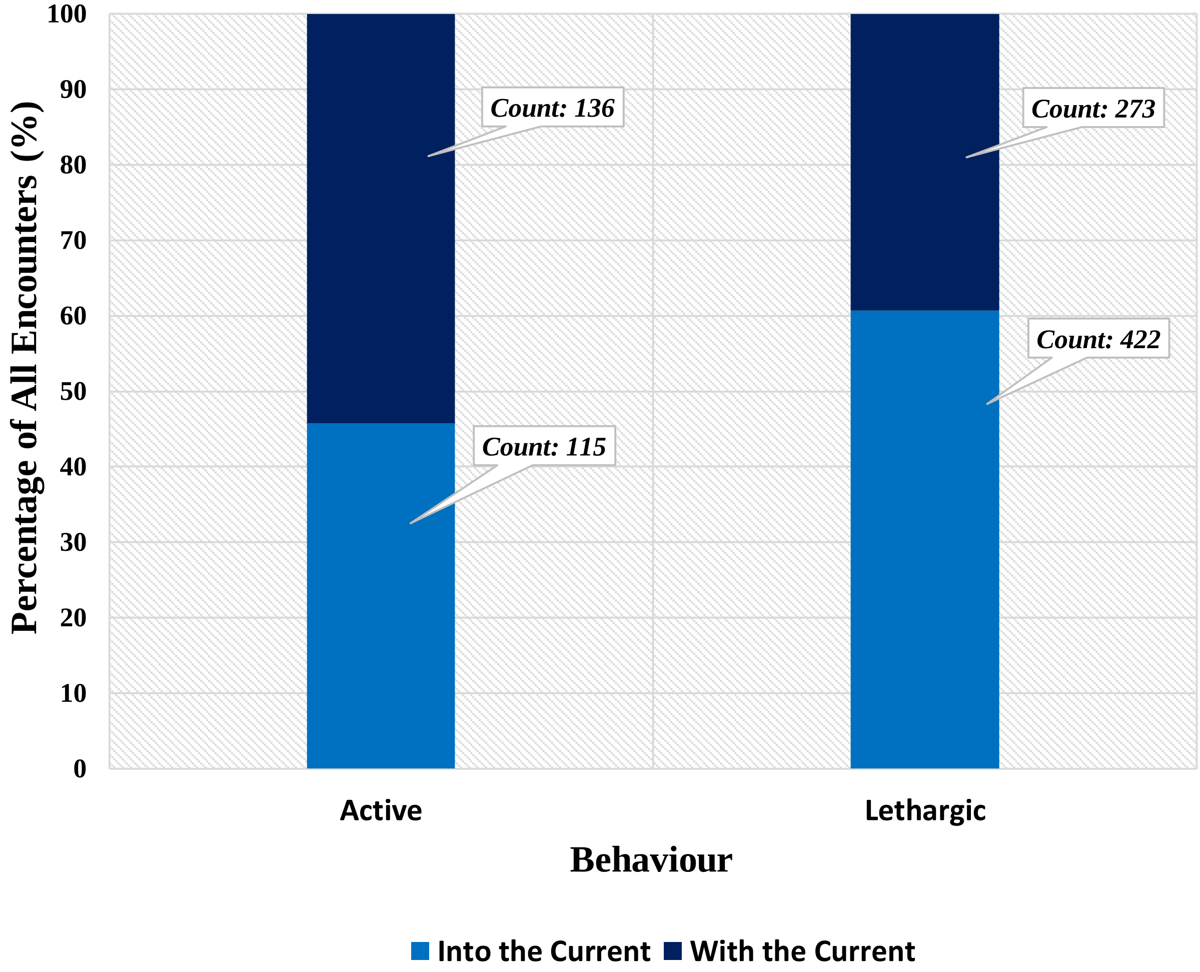

Figure 12. Comparison of active and lethargic whale sharks swimming headlong into the current against those swimming with the current.

There was a significant association between whale shark behaviour and direction of travel (X^2=16.08, df= 1, n= 946, p= 0.001: Appendix 6). Lethargic sharks showed a significantly greater association with travelling headlong into the current than active sharks. Using percentage deviations, the observed frequency of lethargic sharks swimming headlong into the current was 6.5% greater than expected. The observed frequency of active sharks swimming headlong into the current was 19.3% less than expected. Phi and Kendall's tau-b correlation coefficients were similar (Phi= 1.000, p=0.001; tau-b= 0.485, p=0.001: Appendix 6) suggesting there was a nominal correlation between whale shark behaviour and direction of travel. Thus, the hypothesis that a lethargic shark's direction of travel is headlong into the current to reduce the amount of energy required to pass water over the gills during recuperation from a deep dive, is accepted.

4.3. Whale Shark Behaviour and Remora Attachment Likelihood

The number of records for which behaviour of the shark could be classified as well as remora presence or absence having been noted was 2661. Of these records 23.7% (n=632) were active sharks and the remaining 76.3% (n= 2029) were lethargic. Of those sharks classified as active, 23.1% (n=146) were observed with remoras attached and 76.9% (n=486) observed with remoras absent. Of those sharks classified as lethargic, 2.9% (n=60) were observed with remoras attached and 97.1% (n=1969) observed with remoras absent (Figure 13).

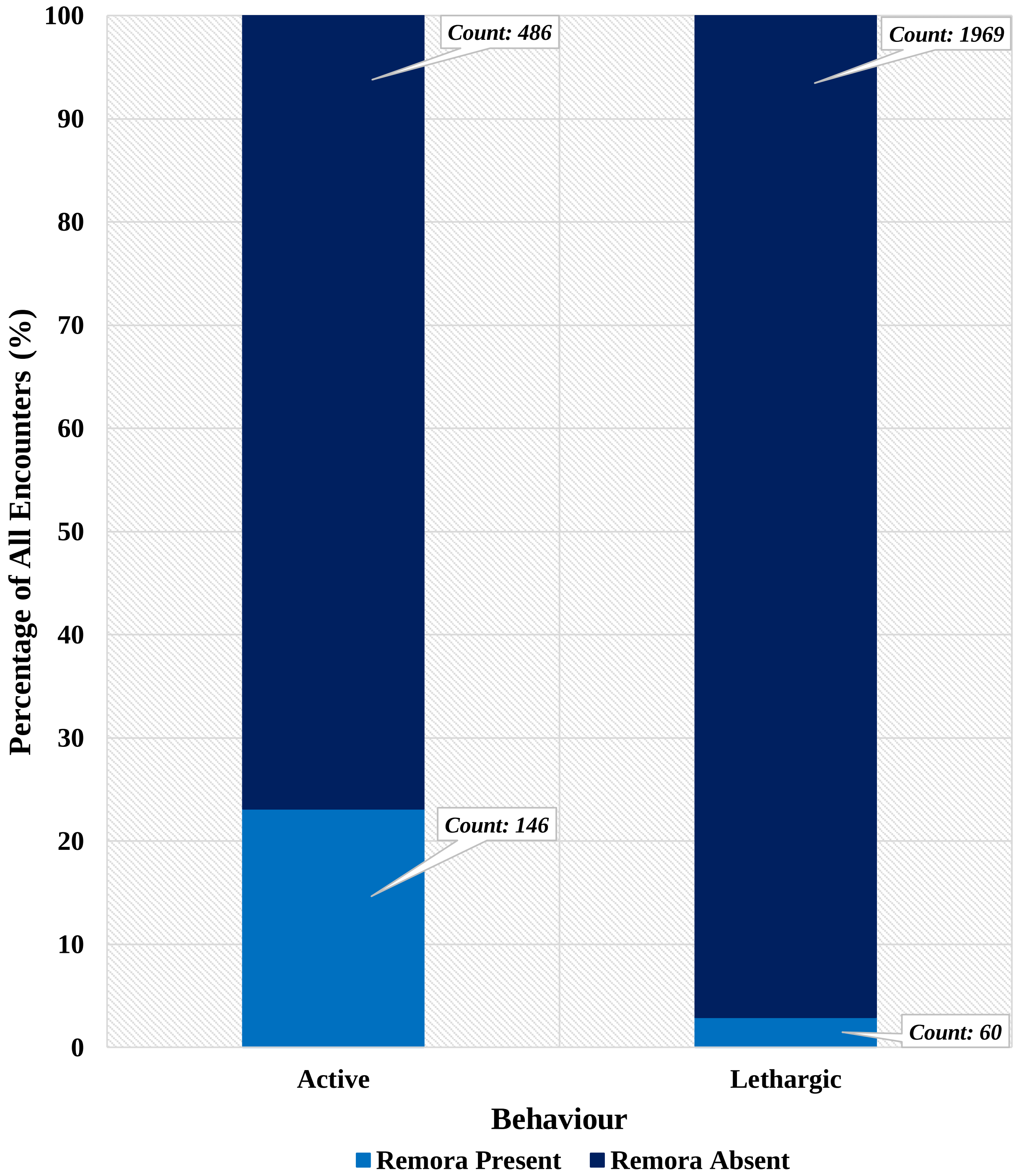

Figure 13. Comparison of active and lethargic whale sharks with remora present against those with remora absent.

There was a significant association between whale shark behaviour and remora attachment (X^2=266.77, df= 1, n= 2644, p= 0.001: Appendix 7). Remoras showed a greater affinity with active sharks than lethargic sharks. Using percentage deviations, the observed frequency of active sharks with remora present was 66.8% greater than expected. The observed frequency of lethargic sharks with remora present was 61.3% less than expected. Phi and Kendall's tau-b correlation coefficients were similar (Phi= 0.036, p=0.001; tau-b= 0.036, p=0.042: Appendix 7) suggesting there was a nominal correlation between whale shark behaviour and remora attachment. Thus, the hypothesis that presence of remora on a shark indicates prolonged surface time and so presumed increase in body temperature and oxygen levels, shown by active behaviour, is accepted.

4.4. Morphological Variables

4.4.1. Shark Size and Behaviour

The number of records for which both shark size and whale shark behaviour were noted was 1984. Of these, 13.2% (n=262) were categorised as small, 82.0% (n=1627) as medium and 4.8% (n=95) as large. Of those sharks categorised as small, 29.4% (n=77) were active and 70.6% (n=185) were lethargic. For medium sharks, 22.9% (n=372) were active and 77.1% (n=1255) were lethargic, and for large sharks, 33.7% (n=32) were active and 66.3% (n=63) were lethargic (Figure 14).

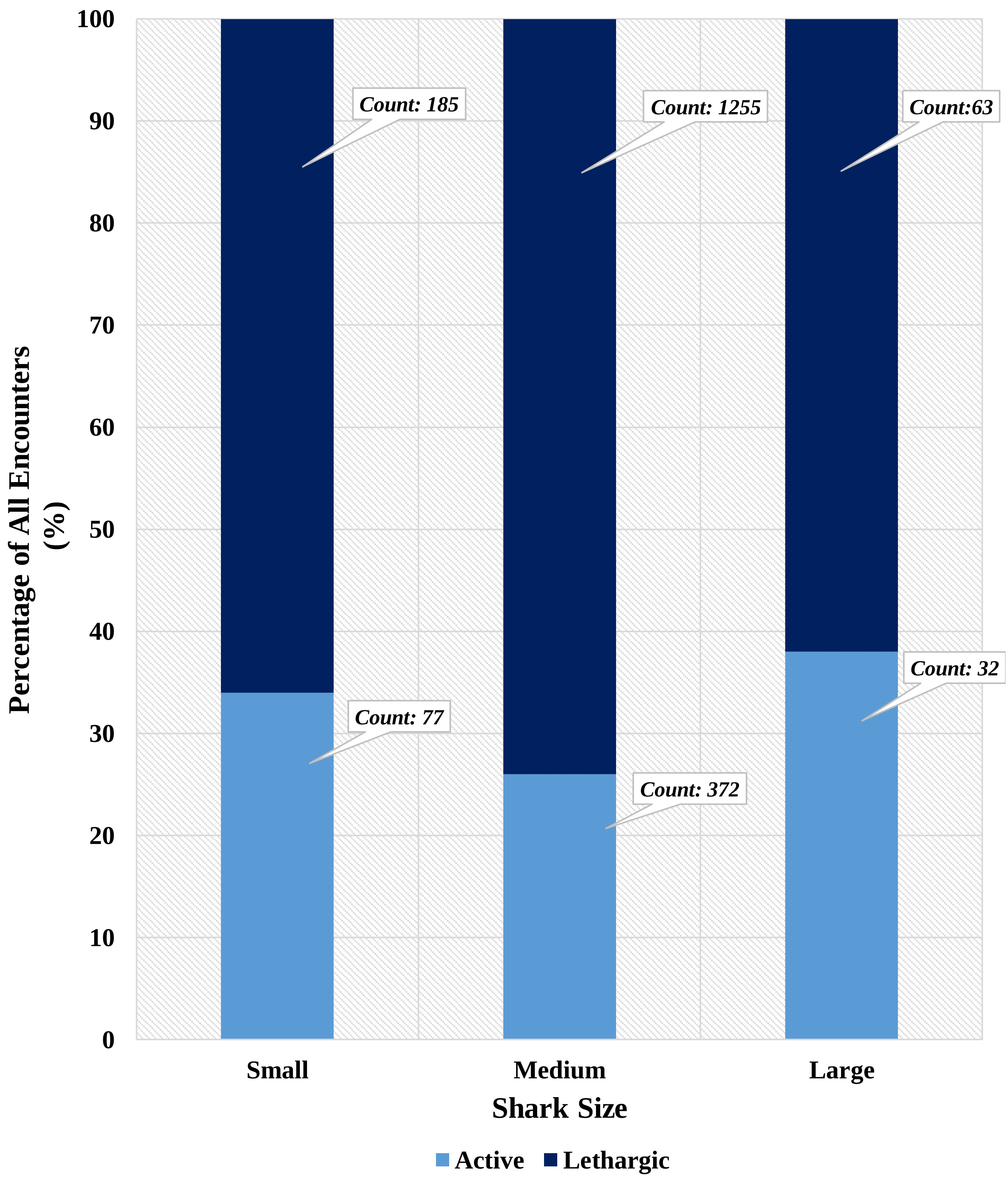

Figure 14. Comparison of shark behaviours displayed by small, medium and large whale sharks.

There was a significant association between shark size and behaviour (X^2=10.07, df= 2, n= 1986, p= 0.006: Appendix 8.1); both small and large sharks showed a higher proportion of active behaviour compared to medium sized sharks. Using percentage deviations, the observed frequency of active behaviour was: 17.6% greater than expected for small sharks; 5.7% less than expected for medium sharks and 21.8% greater than expected for large sharks. Phi and Kendall's tau-b correlation coefficients were similar (Phi= 0.069, p=0.009; tau-b= 0.016, p=0.028: Appendix 8.1) suggesting there was a nominal correlation between shark size and shark behaviour. Thus, a null hypothesis that morphological features of a shark has no effect on shark behaviour, is rejected.

4.4.2 Shark Size and Remora Attachment Likelihood

The number of records for which both shark size and remora presence/absence had been noted was 1984. Of these:

- 13.2% (n=262) were categorised as small, 12.6% (n=33) of which had remora present and 87.4% (n=229) remora absent;
- 82.0% (n=1627) were categorised as medium, 7.9% (n=128) of which had remora present and 92.1% (n=1499) remora absent; and
- 4.8% (n=95) were categorised as large, 4.2% (n=4) of which had remora present and 95.8% (n=91) remora absent (Figure 15).

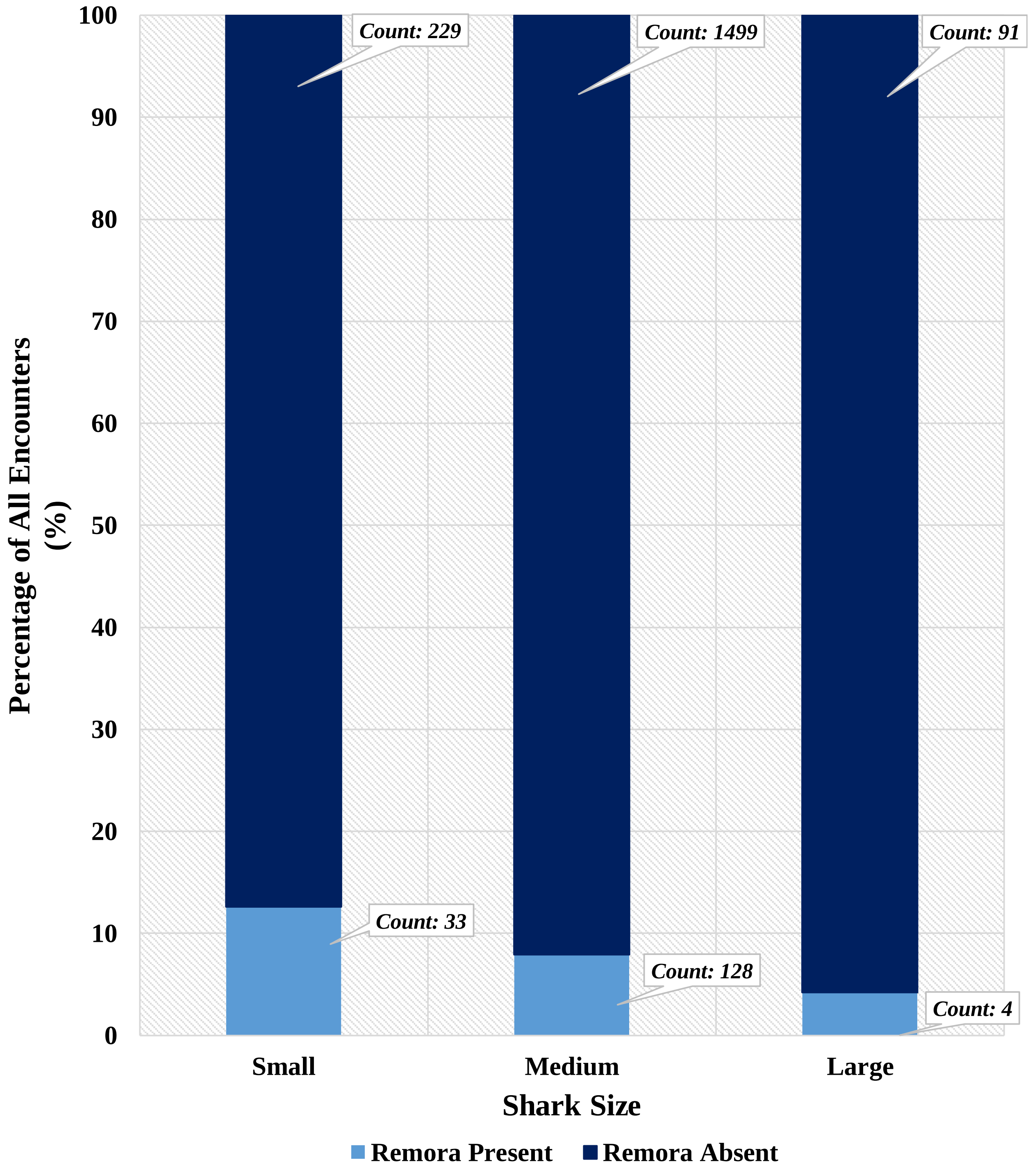

Figure 15. Comparison of whale shark encounters with remora present against those with remora absent, for small, medium and large sharks.

There was a significant association between shark size and remora attachment (X^2=8.82, df= 2, n= 1984, p= 0.012: Appendix 8.2). Remora attachment likelihood was greater when the shark encountered was classified as small (0.5-4m total length). Using percentage deviations, the observed frequency of remora attachment was 33.9% greater than expected for small sharks, 5.4% less than expected for medium sharks and 49.4% less than expected for large sharks. Phi and Kendall's tau-b correlation coefficients were similar (Phi= 0.067, p=0.012; tau-b= 0.065, p=0.006: Appendix 8.2) suggesting there was a nominal correlation between shark size and remora attachment. Thus, a null hypothesis that morphological features of host sharks' has no effect on remora attachment likelihood, is rejected.

4.5. Environmental Variables

4.5.1. Effects of Sea State on Whale Shark Behaviour

A total of 2147 records noted sea state at the time of the encounter. Of these 48.7% (n=1046) were recorded as calm, 26.6% (n=572) as slight, 20.8% (n=446) as moderate and 3.9% (n=83) as rough. Of the sharks encountered during:

- Calm sea states, 23.1% (n=242) were active and 76.9% (n=804) were lethargic;
- Slight sea states, 24.8% (n=142) were active and 75.2% (n=430) were lethargic;
- Moderate sea states, 25.3% (n=113) were active and 74.7% (n=333) were lethargic; and
- Rough sea state, 28.9% (n=24) were active and 71.1% (n=59) were lethargic.

No significant association between sea state and whale shark behaviour was found (X^2= 2.08, df= 3, n= 2147, p= 0.556: Appendix 9.1). Thus, a null hypothesis that sea state has no effect on whale shark behaviour, is accepted.

4.5.2. Effect of Sea State on Remora Attachment Likelihood

Of the 2147 records which noted sea state at the time of the encounter, 1916 had remora presence or absence established. Of these 51.2% (n=980) were recorded as calm, 26.7% (n=512) as slight, 18.4% (n=353) as moderate and 3.7% (n=71) as rough. Of those sharks encountered during the sea state categorised as:

- Calm, 8.1% (n=79) had remora present and for 91.9% (n=901) remora were absent;
- Slight, 16.0% (n=82) had remora present and for 84.0% (n=430) remora were absent;
- Moderate, 5.7% (n=20) had remora present and for 94.3% (n=333) remora were absent; and
- Rough, 16.9% (n=12) had remora present and for 83.1% (n=59) remora were absent (Figure 16).

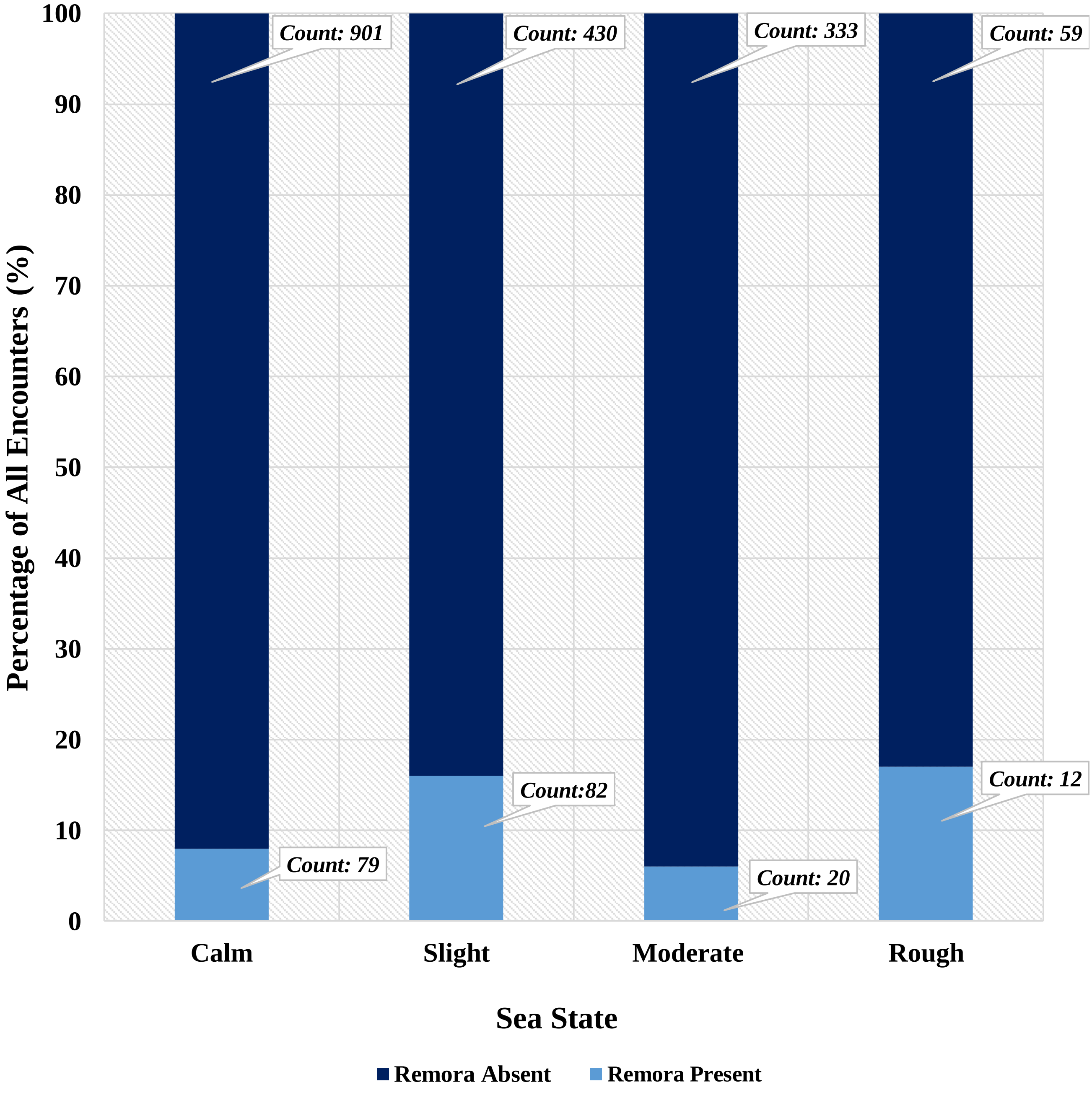

Figure 16. Comparison of whale shark encounters with remora present against those with remora absent for each of the four sea states.

There was a significant association between sea state and remora attachment (X^2= 35.56, df= 3, n= 1916, p= 0.001: Appendix 9.2); remora attachment likelihood was greater in sea states slight and rough. Using percentage deviations, the observed frequency of remora attachment was: 20.0% less than expected during calm sea states; 37.1% greater than expected during slight sea states; 43.8% less than expected during moderate sea states and 40.0% greater than expected during rough sea states. Phi and Kendall's tau-b correlation coefficients were similar (Phi= 0.035, p=0.001; tau-b= 0.038, p=0.062: Appendix 9.2) suggesting there was a nominal correlation between sea state and remora attachment. Thus, a null hypothesis that sea state has no effect on remora attachment likelihood, is rejected.

4.5.3. Effect of Season on Whale Shark Behaviour

The two seasons experienced in the S.A.MPA are: the dry northeast monsoon and the wet southwest monsoon. Of the 2661 shark encounters, 59.1% (n=1571) were had during the dry northeast monsoon season, 23.9% of those sharks were active and 76.1% were lethargic. The remaining 40.9% (n=1090) of the encounters occurred during the wet southwest monsoon season. Of these sharks 22.8% (n=249) were active and 77.2% (n=841) were lethargic. No significant association between season and whale shark behaviour was found (X^2= .425, df= 1, n= 2661, p= 0.514: Appendix 10.1). Thus, a null hypothesis that season has no effect on whale shark behaviour is accepted.

4.5.4. Effect of Season on Remora Attachment Likelihood

Of the shark encounters had during the dry northeast monsoon season, 10.3% (n=162) had remoras present, and for the remaining 89.7% (n=1409) remoras were absent. During the wet southwest monsoon season 3.8% (n=41) of sharks encountered had remoras present and for 96.2% (n=1049) remoras were absent (Figure 17).

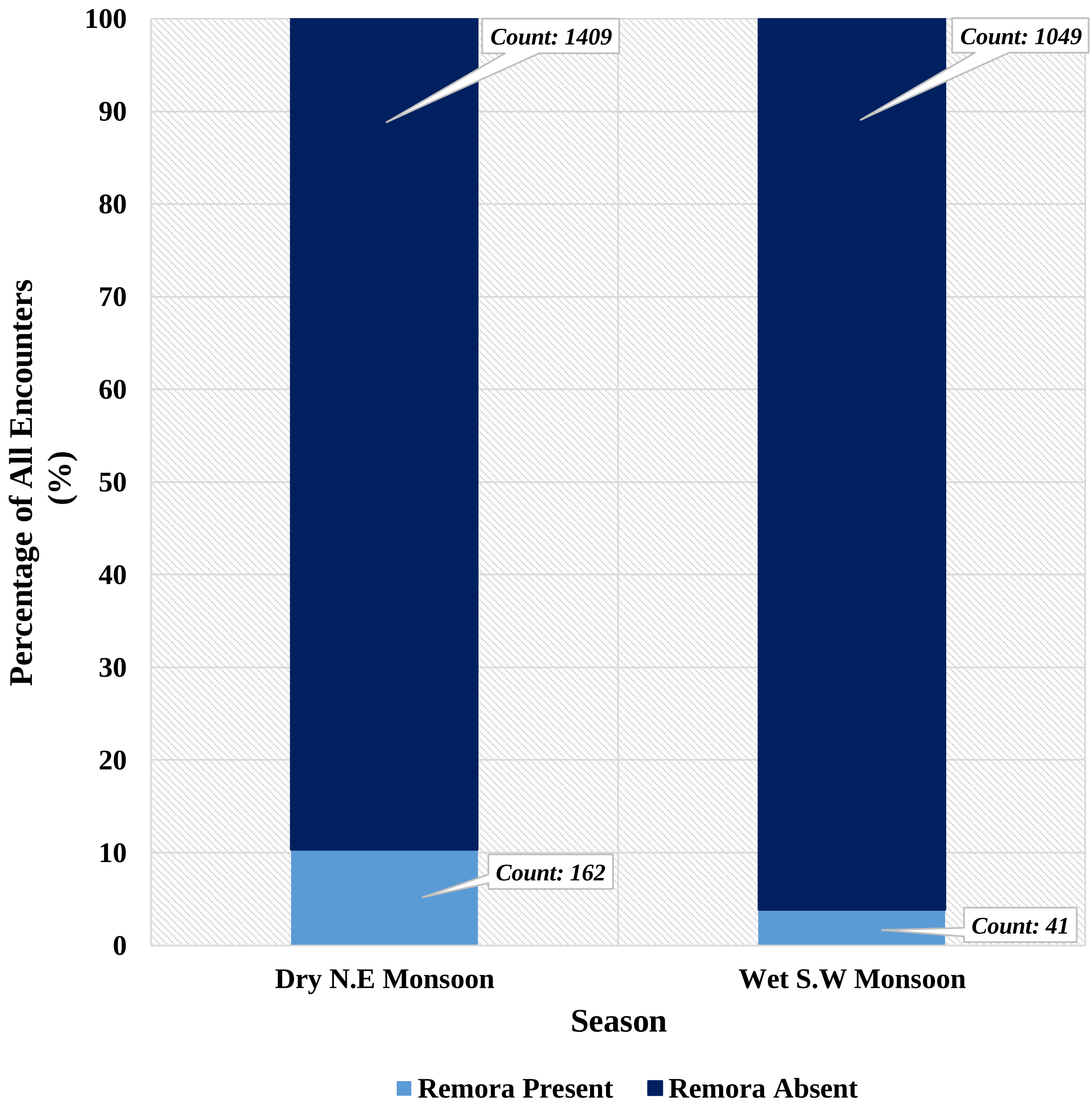

Figure 17. Comparison of whale shark encounters with remora present against those with remora absent between the dry northeast monsoon season and the wet southwest monsoon season.

There was a significant association between season and remora attachment (X^2= 39.18, df= 1, n= 2661, p= 0.001: Appendix 10.2); remora attachment was more likely to occur during the dry northeast monsoon season. Using percentage deviations, the observed frequency of remora attachment was 23.1% greater than expected during the dry northeast monsoon season and 50.7% less than expected during the wet southwest monsoon season. Phi and Kendall's tau-b correlation coefficients were similar (Phi= 0.121, p=0.001; tau-b= 0.121, p=0.001: Appendix 10.2) suggesting there was a nominal correlation between season and remora attachment. Thus, a null hypothesis that season has no effect on remora attachment likelihood, is rejected.

4.5.5. Effect of Sea Surface Temperature on Remora Attachment Likelihood

There was no significant association between sea surface temperature and remora attachment likelihood (U=64957, n= 1239, Z= -891, p= 0.382: Appendix 11). Thus, a null hypothesis that temperature has no effect on remora attachment likelihood is accepted.

Logistic regression analysis was conducted to predict remora attachment likelihood using sea surface temperature as the predictor.

A test of the full model against a constant only model was statistically significant, indicating that the predictor (temperature) did not reliably determine remora attachment likelihood (X^2 = 1515, df=1, p 0.218). The Wald criterion demonstrated that temperature did not make a significant contribution to the prediction (p = 0.220). This model correctly classified 90.2% of cases and explained just 0.3% (Nagelkerke $R^2=0.03$) of the variance in remora attachment indicating no significant relationship between the predictor and remora attachment likelihood (Appendix 14). Thus, temperature is not statistically significant (p=0.220), in determining remora attachment; the null hypothesis is accepted.

4.6. Anthropogenic Variables

4.6.1. Effect of the Number of Boats and Persons Present During an Encounter on Whale Shark Behaviour

There was a significant association between the number of boats present at an encounter and the shark's behaviour (U=95489, n= 1585, Z= -10.009, p= 0.001, two-tailed: Appendix 12.1) and between the number of persons present at an encounter and whale shark behaviour (U=81988, n= 1525, Z= -11.150, p= 0.001, two-tailed: Appendix 13.1). When sharks behaved lethargically there was a significantly larger number of boats and persons present.

Logistic regression analysis was conducted to predict whale shark behaviour using the number of boats and persons present as predictors.

A test of the full model against a constant only model was statistically significant, indicating that the predictors as a set (number of boats and persons) reliably determine whale shark behaviour ($X^2 = 131$, df =2, p=0.001). The Wald criterion demonstrated that both number or boats and persons made a significant contribution to the prediction (p = 0.001). The model correctly classified 85.7% of cases and explained 16.6% (Nagelkerke $R^2=0.166$) of the variance in whale shark behaviour indicating a moderately weak relationship between the predictors and exhibited behaviour. When the number of boats was raised by one unit (one boat), a shark was 0.785 (ExpB=0.785) times more likely to exhibit lethargic behaviour and when the number of persons was raised by one unit (one person), the shark was 0.953 (ExpB=0.953) times more likely to exhibit lethargic behaviour (Figure 18: Appendix 15). Thus, a null hypothesis that the number of boats and persons present at an encounter has no effect on whale shark behaviour, is rejected.

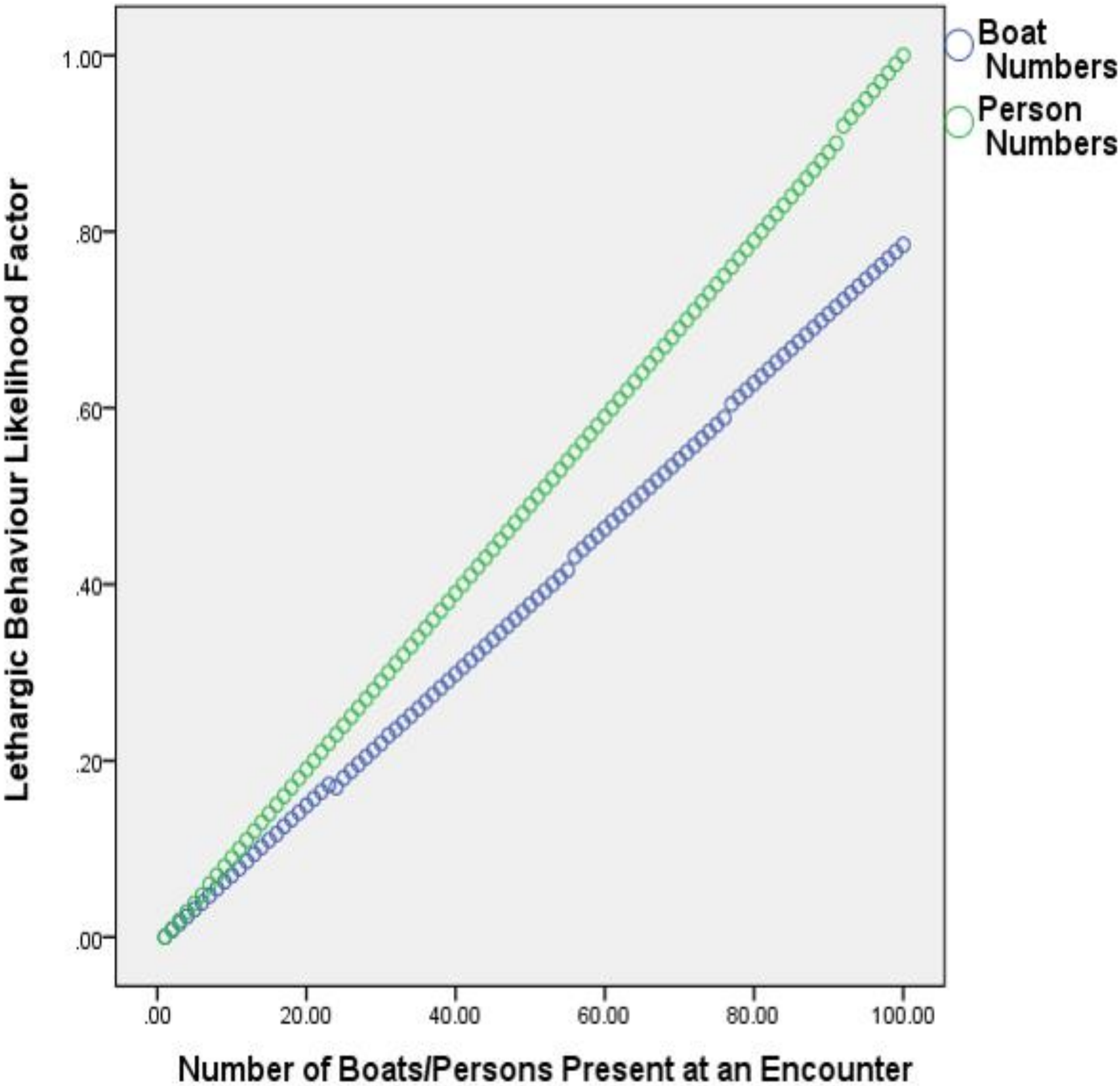

Figure 18. Lethargic behaviour likelihood factor in relation to the number of boats and persons present during an encounter created in SPSS.

4.6.2. Effect of the Number of Boats and Persons Present During an Encounter on Remora Attachment Likelihood

There was a significant association between the number of boats present at an encounter and remora attachment likelihood (U=83159, n= 1585, Z= -7.427, p= 0.001, two-tailed: Appendix 12.2) and between the number of persons present at an encounter and remora attachment likelihood (U=60983, n= 1525, Z= -9.156, p= 0.001, two-tailed: Appendix 13.2). When remoras were present there was a significantly smaller number of boats and persons present.

Logistic regression analysis was conducted to predict remora attachment likelihood using the number of boats and persons present as predictors.

A test of the full model against a constant only model was statistically significant, indicating that the predictors as a set (number of boats and persons) reliably determine remora attachment likelihood (X^2 = 99, df=2, p=0.001). The Wald criterion demonstrated that both number or boats and persons made a significant contribution to the prediction (p = 0.001). The model correctly classified 89.7% of cases and explained 14.6% (Nagelkerke $R^2=0.146$) of the variance in remora attachment likelihood indicating a moderately weak relationship between the predictors and presence/absence of remora. When the number of boats was raised by one unit (one boat), remora attachment was 1.239 (ExpB=1.239) times less likely and when the number of persons was raised by one unit (one person), remora attachment was 1.055 (ExpB =1.055) times less likely (Figure 19: Appendix 16). Thus, a null hypothesis that the number of boats and persons present at an encounter has no effect on remora attachment likelihood, is rejected.

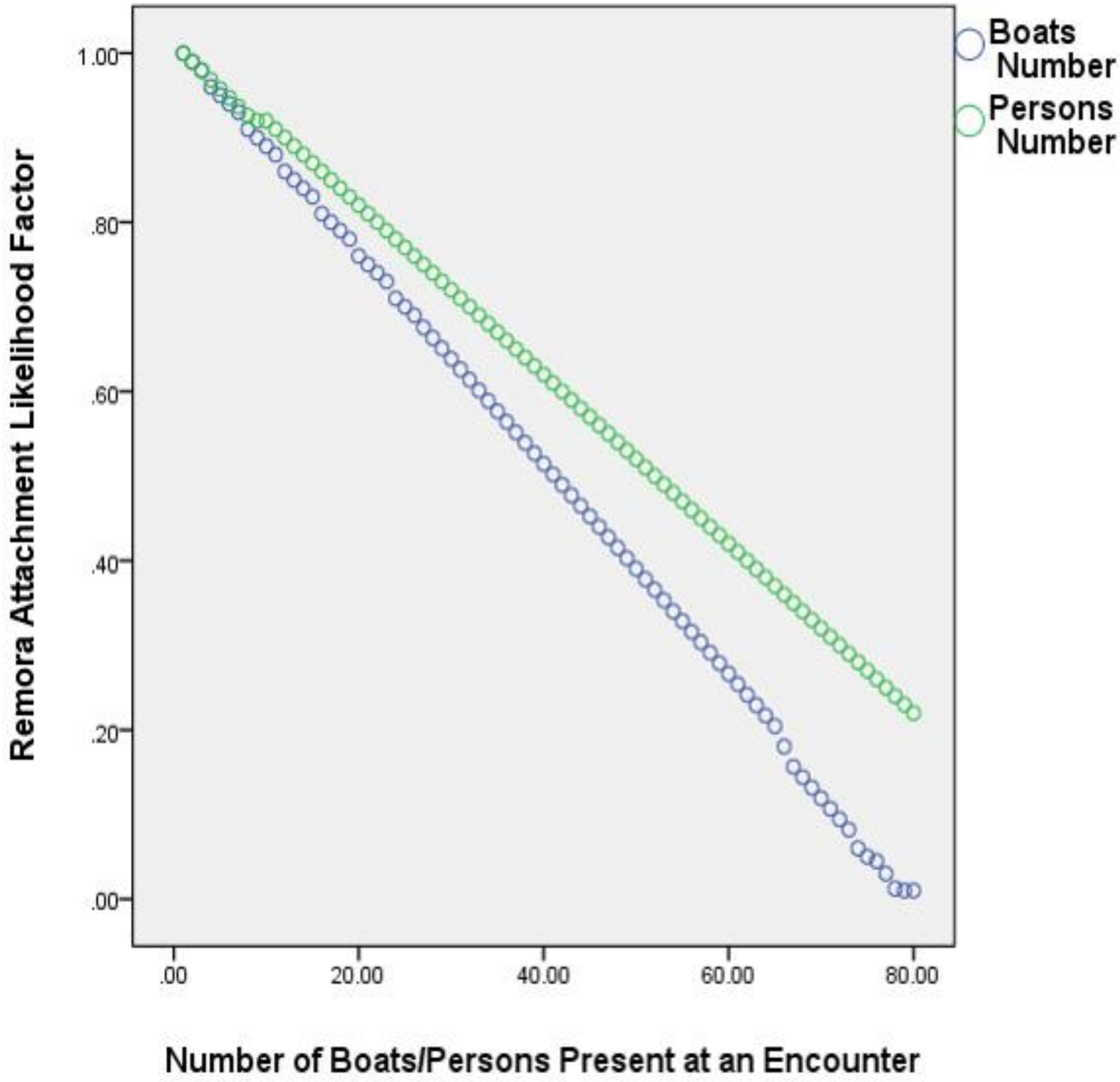

Figure 19. Remora attachment likelihood factor in relation to the number of boats and persons present during an encounter created in SPSS.

5. Discussion

5.1. Whale Shark Behaviour and Direction of Travel

Lethargic sharks, who are assumed to have recently ascended from deep dives and are thus recuperating, showed a greater association with travelling headlong into the current than active sharks, assumed to be in a state of equilibrium. This result indicates that those sharks which frequent the S.A.MPA are experiencing metabolic consequences from deep dives (Thums *et al.,* 2013) where redox conditions experienced are hypoxic or anoxic Kamykowski, 1990; Hennemann, 2001) requiring the sharks to ascend and re-oxygenate. Therefore, recuperating sharks may purposefully travel in this direction, knowingly reducing the amount of energy expenditure required to pass water over their gills. This result further highlights the importance of the S.A.MPA as a vital habitat utilised by this species during necessary recuperation following deep dives, essential for the efficient functioning of these sharks' metabolic processes.

However, this result may be a mere representation of human judgement as opposed to accurate analysis of the behaviours recorded: the behaviours recorded within the master excel sheet of data used in this study is an accumulation of many people's observations. Whilst the behaviour recorded is the behaviour observed, this may not be a true description of the behaviour performed due to inaccurate empirical interpretation. To illustrate this further: a shark which is swimming headlong into the current has to contend with the frictional force of said current, and thus expend more energy, whereas a shark swimming with the current is aided in its movement. Therefore, a shark swimming into the current may be recorded as lethargic due to an observed, slow swimming speed when in reality this shark is active, expending great amounts of energy as it contends with the frictional forces exerted on it from the current. Thus, the margin for error in the raw data set can be considered an influential bias in the results. This could be overcome by calculating tail swipes per minute and distance travelled, giving an estimate of speed and thus a quantified measure of the effort exerted by a shark.

In addition to this the movements of any animal are governed by a multitude of both internal and external stimuli. The behaviour of a shark is influenced by a multitude of factors including the general health and condition of the individual; light levels; water mass; geographic locations; geomagnetic gradient; oxygen levels, and abundance of prey (Speed *et al.,* 2010). It must also be noted that explanations for surface swimming include using the Earth's dipole field and celestial signs in navigation (Klimley *et al*., 2002) therefore there is potential that some of the sharks observed in this region were in fact not displaying recuperation behaviours at all. Thus, the complexity which comes with accurately determining and explaining a shark's behaviour is great. In addition to this, to fully understand a natural behaviour, individuals should be observed for extensive periods of time which is not always feasible, especially in the study of a species whose natural habitat is uninhabitable by humans. Therefore, the knowledge possessed today regarding the logic behind a shark's behaviour is somewhat of an enigma.

5.2. Whale Shark Behaviour and Remora Attachment Likelihood

Remora attachment likelihood was far greater when a shark showed active behaviour. This result provides further evidence that remora may be more likely to attach to active sharks because of the swift passage of water over the remoras' gills facilitated by the faster movement of their host (Bohlke and Chaplin, 1993). Additionally, this result gives statistical significance to the theory that remora are predominantly found attached to active sharks due to the opportunity of attachment being greater. As these sharks have been within the remoras' depth range longer, they are more fully recuperated due to a longer surface interval from deep dives, which enables them to swim actively. Thus, consequently remora attachment can be assumed a non-invasive associative method for classifying the recuperation level of the host shark. This theory, however, is yet to be explored in any other form; there is no accompanying evidence to provide validation of this finding.

Remora attachment has been found to negatively impact the host acting as a hydrodynamic parasite; their presence disrupts the flow of water over the hosts' body potentially increasing drag (Domenici, 2010). Spinning aerial leaps performed by spinner dolphins (*Stenella longirostris*) has been suggested a behavioural response to remora attachment and an attempt to forcibly remove them from their skin (Fish *et al.,* 2006). Such response has been documented in other species such as black tip sharks (*Carcharhinue limbatus*) who jump in what is an assumed attempt to dislodge remora (Ritter, 2002). Therefore perhaps the active behaviour observed in whale sharks is a behavioural response to remora attachment as opposed to a stimulus for remora attachment.

5.3. Morphological Variables

5.3.1. Effect of Shark Size on Whale Shark Behaviour

Active behaviours were more regularly observed in sharks classified as small and large. This is somewhat of an unexpected result which is difficult to explain; in the early developmental stages of all elasmobranchs, superficial external gills are present in addition to the true gills (Hughes, 1965). Though it is yet to be proven, it is possible that these provide smaller sharks with an advantage, enabling them to recuperate from oxygen depletion faster and thus be more readily active.

Perhaps this pattern reflects the lack of deep foraging experience in the younger sharks, meaning the smaller juveniles simply do not dive to depths as great as those who are older, larger and more experienced, meaning recuperation time, need not be so long. Such variation in vertical displacement has also been observed among size classes of juvenile white sharks in the eastern Pacific, with larger juveniles making deeper vertical excursions than young-of-the-year (Weng *et al.*, 2007). This could arise because of the relatively greater thermal tolerance of larger individuals, allowing them to better withstand cooler temperatures. This does not account, however, for the separation of medium classed whale sharks. Telemetry devices to estimate movement rates by distance travelled over certain time periods could help certify differences in behaviour depending on shark size.

5.3.2. Effect of Shark Size on Remora Attachment Likelihood

Remora attachment likelihood was greater when the shark encountered was classified as small (0.5-4m total length). This is a second unexpected result. Remoras will often seek refuge in the spiracles, mouth, or gill cavities of sharks (McClane, 1998), and it has been theorised that the host acts as a facilitator of chance encounters with mating partners for the remora (Martins and Ivan, 2003). Thus, it is logical to assume that remora preference would be for larger host sharks' providing greater surface area on which to hide and socialise in reproductive strategies. Remora host preference has been largely unexamined; knowledge consists of preferred host species but is not specific to any great extent between individuals within that species. Carvalho-Filho (1999) showed this particular species of remora (*Remora remora*) preferentially attached to juvenile turtles in the South-West Atlantic. Johnston *et al.* (2014) showed the comparable species, *Remora australis*, demonstrated preference for female and adult spinner dolphins as opposed to males and other age groups. This knowledge, whilst limited, suggests host preference may be species specific or geographical. It must also be considered that host availability is a dominant factor in predicting attachment.

5.4. Environmental Variables

5.4.1. Effect of Sea State on Whale Shark Behaviour

No significant association was found between sea state and whale shark behaviour. Thus, if whale shark behaviour is inferential of the duration of surface interval time following a deep dive it can be denoted that this behaviour, in terms of oscillatory vertical displacement, is not influenced or changed in any manner by sea state and is a regular pattern displayed by these sharks as documented elsewhere (Gunn *et al.*, 1999, Wilson *et al.*, 2006). There is potential, however, for this result to be inaccurate due to observational error when determining sea states.

5.4.2. Effect of Sea State on Remora Attachment Likelihood

Remora attachment likelihood was greater in sea states classified as slight and rough. The effect of sea state having a significant impact on Echeneidae behaviour is vastly unexplored. As it is unclear what the ecological or biological reason for this result is, it may simply be down to chance. Whale shark sightings have been subjectively noted by MWSRP to peak during times of strong tidal flows; this may account for the greater observed attachment of remora during rough sea states, as there are potentially more available host sharks. This does not, however, account for the significant association between remora attachment and whale sharks during slight sea states. The result could be explained if the majority of recorded encounters were during slight or rough sea states, thus increasing the chance of remora attachment being observed, yet this is not the case. Just 30.4% (n=583) of all records were during both slight and rough sea states combined, so the figures needed to support this explanation are not reflected within the data. Again this result may be a representation of observational error as opposed to an accurate description of sea states. Whilst all records were kept at a level of accuracy through validation by the experienced co-ordinators, co-ordinators changed over the 10 year operating period of MWSRP and not all encounters were validated due to having been submitted by accompanying bodies. Interpretation between two levels of sea state, slight and moderate for example, will of course be subject to observer bias.

5.4.3. Effect of Season on Whale Shark Behaviour

No significant association was found between season and whale shark behaviour. Thus, again if whale shark behaviour is inferential of the duration of surface interval time following a deep dive, it can be denoted that this behaviour, referring only to oscillatory vertical displacement, is not influenced or changed in any manner by season.

5.4.4. Effect of Season on Remora Attachment Likelihood

Remora attachment was more likely to occur during the dry northeast monsoon season. Despite whale shark and remora residency in the S.A.MPA not being seasonal, this result may be explained by the coinciding tourism industry seasons. This industry, on which many of the associate bodies that contributed to the data set depend, experiences a high and low season. High season coincides with the dry northeast monsoon season. This may explain why remora attachment was deemed more likely to occur during this period; more personnel are out on the water increasing the chance of encounters for inclusion in the data set. This increased chance of whale shark encounters also means an increased chance of observing their phoretic relationship with remora. It must be remembered that the raw data set is inclusive only of those sharks which have been surveyed and does not include all the sharks that frequent the area. In turn this means that the data set does not reflect all associations between whale sharks and remora, only those which have been observed. Therefore, the result may be a reflection of participation effort, subject to bias of unequal sampling across the study area and period; nothing certain is known about the intervening gaps in space and time. This may be a source of strong inaccuracy in the results and can thus lead to incorrect predictions.

Evidence which supports the idea that this result is a reflection of participation effort, and can therefore not accurately deem season to be an influential factor in remora attachment likelihood, includes habitat suitability maps. Habitat surveys have indicated the opposite season, the wet southwest monsoon, would bring greater numbers of whale sharks due to higher primary productivity during this time (Speed, 2010). Additionally, the wet south west monsoon season experiences less stable weather with stronger tidal flows which have been subjectively noted by MWSRP as peak times for whale shark sightings. A stronger Southern Oscillation Index (SOI) positively influenced whale shark abundance at Ningaloo Reef. This may reflect changes in the strength of oceanographic processes such as the Leeuwin Current and current-driven upwelling which may affect the abundance of whale sharks transported to the region and the availability of their prey by driving productivity changes (Sleeman, *et al.*, 2010). There is potential for this phenomenon to be attributed to the differing seasonal observed whale shark abundance within the S.A.MPA, though this is yet to be investigated.

5.4.5. Effect of Sea Surface Temperature on Remora Attachment Likelihood

No significant association was found between sea surface temperature and remora attachment likelihood. Therefore, the potential for remora to attach to a whale shark is neither hindered nor promoted by differing sea surface water temperatures. This can be explained by natural selection; over the course of this species evolution, it has become best suited to its environment, adapted to tolerate the naturally fluctuating temperatures experienced in the Indian Ocean. Therefore, it is logical to assume its diel behaviour would not be affected by changes of this kind.

5.5. Anthropogenic Variables

5.5.1. Effect of the Numbers of Boats and Persons Present During an Encounter on Whale Shark Behaviour

Whale sharks were more likely to behave lethargically when there was a significantly larger number of boats and persons present. By recognizing the reactions of sharks to surrounding human presence, it is possible to hypothesise an empirical level of behavioural conditioning of the whale sharks. Thus, this result infers that whale sharks within the S.A.MPA showing little evasion, are habituated to human presence and have formed a degree of tolerance towards human activities.

It must also be theorised, however, that such behaviour could be induced when a shark enters the S.A.MPA and is subject to eco-tourism activities; the degree of lethargy may be a response to obstruction caused by the high number of boats and persons present, consequently forcing the shark to behave in this manner. Encounters could often have $\geq$100 persons present in the water, swimming behind, in front of and below the shark (R. Goddard *pers. obs.* 2015). This theory would be extremely difficult to test as it is impossible to accurately interpret and explain the behaviours of other species. Additionally, this theory can be easily challenged; if the whale shark wanted to avoid the obstruction, it would simply retreat by diving to depths inaccessible to humans.

It has been observed by MWSRP that sharks frequenting the S.A.MPA display variable behaviour as humans enter the water. On occasion the shark will stay in the vicinity for long periods, whereas other sharks will descend as soon as they are aware of anthropogenic activity. Therefore, the effect of such on a shark's behaviour, may be unique to each individual shark and a reflection of their "personality", however, analysis of this idea is yet to be conducted. It must also be noted, that a single invasive act such as a tourist touching the shark, attempting to ride the shark or using flash photography close to the cranial region will cause the shark to behave evasively, ostensibly to avoid further harassment, regardless of prior behaviour. From this knowledge, individual histories with human contact may account for differing behaviours in sharks; those who have been subjected to harassment or have obtained injuries from collision with vessel propellers may be more evasive and actively avoidant to anthropogenic activities due to negative association. Thus their behaviour may be a result of their past histories and unique to the individual as opposed to the species' natural demeanour.

5.5.2. Effect of the Number of Boats and Persons Present During an Encounter on Remora Attachment Likelihood

Remoras were more likely to be observed attached when there was a significantly smaller number of boats and persons present. This result infers that increased vessel traffic and human activity act as deterrents towards attachment for this species. Possible reasons for this include the increased background noise produced by such things as continuous boating and bodily movements, having negative effects on these fish. There are concerns that less intense but longer lasting sounds such as these, result in the masking of biologically important sounds, hearing loss and stress responses in the immune system of fish, altering their behaviour (Popper *et al.*, 2003). However, despite increasing interest in the effects of sounds on fishes, this issue has only been addressed on the most limited scale and only a few species of fish have been studied. Whether or not these effects are apparent in remora is yet to be confirmed.

It must be noted that *Remora remora* are typically an off-shore species, often observed in greater numbers at night (Sazima *et al.*, 2006); remora are predominantly observed as an accompaniment of sharks during night feeding activity in the nearby Huvadhoo and Thaa atolls of the Maldives. This highlights the importance of other variables such as the diel behaviour of remora as a determinant in the likelihood of observing them attached to whale sharks.

6. Summary

To summarise, the main findings of this study further highlight the importance of this region as a vital habitat for whale sharks. The direction of travel by those whale sharks which frequent the S.A.MPA may be indicative of recuperation behaviour following deep dives, inferring the importance of this region to their metabolic functioning. This may consequently lead to the improved adherence to the code of conduct by tourism vessels and personnel within the S.A.MPA. If a shark is seen swimming headlong into the current this may well indicate the greater need for this shark to be left alone, or the implementation of controls over the number of eco-tourism companies which may engage with that particular shark. Potential human harassment may cause it to re-descend prematurely before it has sufficiently recuperated to the state of equilibrium, subsequently causing negative effects on its metabolic functioning.

Remoras can only frequent this area because the sharks do; their occurrence is dependent on the presence of suitable host species. However, the species *Remora remora* is categorised as a species of "Least Concern" meaning it has been evaluated against the criteria and does not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened (IUCN, 2000). It is common worldwide (Heemstra 1986) with no known major threats or species-specific conservation measures currently in place. Therefore, conservation efforts within the S.A.MPA would be inconsequential to the survival of this species as they are abundant elsewhere.

7. Conclusion

The theory that remora attachment is indicative of a shark's level of recuperation remains ambiguous. Whilst the results here suggest there is a significant association between active sharks and remora presence, additional results suggest alternative variables including: environmental; behavioural; morphological and anthropogenic, in both whale shark behaviour and remora attachment likelihood. Thus, the results are not conclusive enough to neither validate, nor reject this theory.

Considering how little previous research has been conducted into testing the theory of remora attachment as indicative of the recuperation level of a shark, challenges arise when trying to ascertain significance of the results as valid comparisons cannot be made. Thus, the findings presented here should be regarded merely as preliminary indications to potential associations in need of further investigation.

In addition to this, not all stimuli, which almost certainly play a role in influencing whale shark behaviour or remora attachment likelihood have been investigated, therefore the results are not exhaustive enough from which to draw any scientifically grounded conclusions. It is still possible that remora attachment is governed simply by host availability.

7.1. Study Limitations and Improvements

This study only explores the phoretic relationship between juvenile whale sharks and remoras. Whilst it is not known specifically why adults do not frequent this area, it can be associated with the knowledge that home range size generally increases with body size (Speed *at el.*, 2010). In order to draw more accurate conclusions about the relationship between these two species as a useful scientific tool, research would need to be conducted on a wider scale, in relation to both age and geographical range of this shark.

Whilst records of encounters are kept to a reasonably high level of continuity by overseeing supervisors, this could not be regulated extensively; supervisors have changed over the ten year operating period of MWSRP and some whale shark encounter records are made by associate bodies. This may account for some of the more ambiguous results which are a reflection of bias in the data. This also explains why sea surface temperature was not tested against whale shark behaviour as the number of encounters containing both these variables was insufficient.

Survey effort could not be weighted by transect distance covered due to the nature of response to whale shark sightings; data was collected via adaptive survey methods therefore it was not possible to quantify the abundance of encounter ratios. Should a different approach be taken, such as passive surveying along a transect line, this could help in better monitoring the whale shark population of the S.A.MPA.

Surveying is not homogenous in both space and time due to a lack of human resources; therefore, there are intervening gaps in the records which may cause misrepresentation in the data and subsequent results. This limitation could be overcome by increased funding for MWSRP, allowing them to conduct their research continuously throughout the year.

The classification of a shark as active or lethargic was subject to interpretation. This was especially true when two contradictory behaviours were noted, and determining the dominant was difficult. Records were also not always detailed enough and photographic evidence not always sufficient to accurately conclude if remoras were present. This may have led to errors in the calculation of initial results.

There is also the issue of anthropogenic pressures which mean it cannot be accurately determined if the behaviour observed is the animals' true natural behaviour. Whilst it is practically impossible to measure the level of habituation of an individual shark which would account for this bias in the data, it could be accounted for by controlling the number of boats and persons present at an encounter.

Practical limitations included reduced water visibility on certain days. This had two implications: firstly, the data set does not account for all sharks in the region, as only those who were observed are included. Secondly, shark encounters lasted different times- reduced visibility meant an encounter would end sooner than it would have done on a day with increased visibility so the subsequent recorded behaviours of each individual shark are subject to duration. Thus, the dominant behaviour may have been missed.

It was originally planned to explore whether size of remora affected attachment likelihood, hence why size of remora is included in the second page of the encounter sheet (Appendix 3). However, as only two encounters of the 25 experienced in situ had remoras present and at no point in the historical data set is remora size noted, this was no longer possible.

Efforts were made to film each shark from the rear using a GoPro in order to calculate tail swipes per minute giving an estimate of speed. Due to the high number of tourists sharing encounters, which could often reach ≥100 persons, this was often not possible. The footage that was obtained is predominantly disrupted, making it insufficient evidence from which to calculate accurate number of tail swipes. Without this measurement the ability to correctly classify a shark as active or lethargic was limited.

Considering the diel activity patterns of remora, the study design was not fully appropriate for quantifying the relationship between the two species. This indicates the potential for the results presented here to be unreliable. To overcome this limitation surveys should be conducted at night, when remora are noted as more active (Sazima *et al.,* 2006) yet this was not possible due to health and safety issues.

Whilst this study is based on a relatively new and highly unexplored theory resulting in a scarcity of previous research to inform, it has gone some way to explore the patterns of remora attachment to whale sharks.

7.2. Future Research

In order to validate the associations highlighted here, further research into the potential phenomenon that remora attachment is indicative of recuperation levels in sharks, is required. There are many possible determinants for both whale shark behaviour and remora attachment, only a few of which have been explored in this study. In order to expand the knowledge, these would need to be tested extensively, on a larger scale, equally in both space and time, with the aid of more sophisticated technology such as telemetry, tagging devices and thermal imaging cameras.

This study may therefore be considered a precursor for more in-depth research, not only into this association as a method for determining a shark's recuperation level, but also the impacts of eco-tourism on both whale sharks and remoras within the S.A.MPA.

Eco-tourism took over from the hunting of whale sharks as a significant source of income for Maldivians in 1995 (Norman, 2005). Despite this industry raising awareness of the species, thus, contributing to its conservation, there may be secondary concerns for the effects of such anthropogenic activities on these highly mobile animals; their ability to relocate makes this species susceptible to anthropogenic impacts. To mitigate potential anthropogenic stressors caused by the high levels of ongoing eco-tourism within the S.A.MPA, and ensure such activities do not have adverse effects on the behaviour of whale sharks, monitoring must continue as a priority.

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Appendix 1

Directive GPS points for the Maamigilli-Dhigurah Reef.

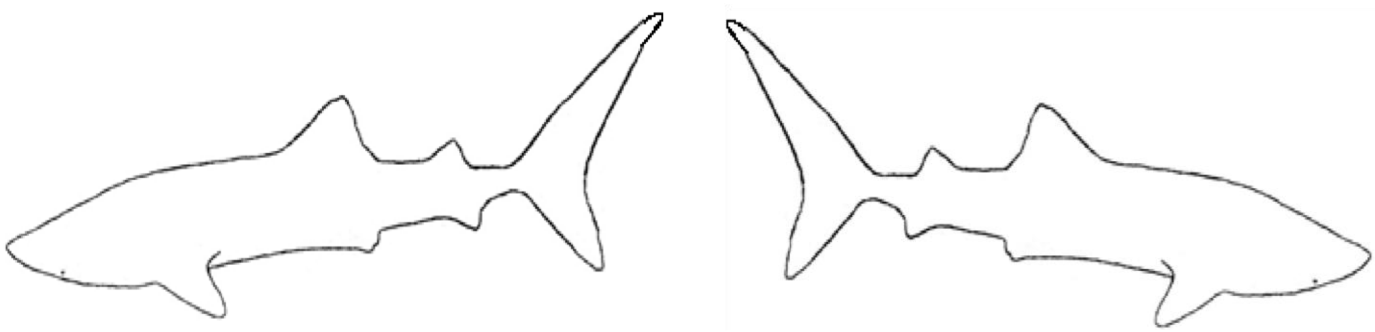
3 38’ 10”N, 72 42’ 18”E / 2. 3 37’ 46”N, 72 42’ 00”E / 3. 3 36’ 44”N, 72 42’ 43”E / 4. 3 35’ 13”N, 72 43’ 20”E 5. 3 34’ 17”N, 72 42’ 54”E / 6. 3 33’ 05”N, 72 42’ 47”E / 7. 3 30’ 16”N, 72 43’ 31”E / 8. 3 29’ 44”N, 72 44’ 00”E / 9. 3 29’ 20”N, 72 46’ 22”E 10. 3 28’ 18”N, 72 48’ 17”E / 11. 3 28’ 07”N, 72 51’ 24”E / 12. 3 29’ 59”N, 72 54’ 17”E / 13. 3 32’ 15”N, 72 55’ 58”E

Appendix 2

Example Data Sheet Page 1.

MWSRP Whale Shark Encounter Sheet

Name of Researcher	Date	Time Start Searching	Time Stop Searching	Breaks (Hrs)!	Encounter Number
					________OF_______
Time Encounter!	**Duration Encounter!**	**Location**	**Coordinates North!**		**Coordinates East!**
Whale Shark ID if Known	**Est Length To 0.5m**	**Tape Length(s)**	**Sex**	**Swim direction**	**Distinguishing Features (e.g. injury type + severity)**
Photographs					
Left I.D	Right I.D	LZR	Scars	Pelvic	



WHALE SHARK BEHAVIOURAL INFORMATION					
Swimming	**Diving**	**CoD**	**Feeding**	**Other Wildlife**	**Other Behaviours**
Slow Fast Banking	Gradual Steep Parabola	Circular Gradual Parabola	Before: Y N During: Y N After: Y N		

HUMAN – SHARK INTERACTION						Reef depth
Persons start	**Persons Max**	**Boats start**	**Boat max**	**Distance to closest boat**	**Swimmers CoC**	
					<4m distance Touch Obstruction Flash photo	

Sea T°	Wind lirection	Wind Speed	Cloud cover	Sea state	Visibility (meters)	Current	
						In	out
						N03° E72° Time:	N03° E72° Time:

Notes:

How did the encounter end:

Appendix 3

Example Data Sheet Page 2.

Behaviour Types		
Feeding:	Ram Filter	Suction
Cruising	Inquisitive	Evasive

Speed	Distance/Time.	Tail Swipes per min.

Activity Level

1 2 3 4 5

Very Passive *Highly Active*

Remoras			
Est. No# at Start of Encounter			
Est. Lengths	0-1ft =	1-2ft =	2-3ft =
Est. No# at End of Encounter.	Same	Increased	Decreased
Obvious Human Impact	Yes	No	

NOTES:

Appendix 4

Master Excel Sheet of All Encounters.

Appendix 5

GPS readings of the 25 encounters from 20 day In-situ data collection period.

Northing	Easting
3.2947	72.53614
3.28937	72.5297
3.29893	72.54178
3.29483	72.53709
3.29359	72.5354
3.29557	72.53851
3.31417	72.54082
3.29261	72.45752
3.2919	72.4511
3.28609	72.47365
3.29329	72.45581
3.29369	72.44782
3.29299	72.45399
3.2924	72.46433
3.30925	72.55119
3.30534	72.54803
3.29916	72.54215
3.30496	72.54771
3.30343	72.54655
3.3048	72.54749
3.28008	72.50057
3.29035	72.53091
3.30194	72.54482
3.30081	72.54397
3.30193	72.54479

Appendix 6

SPSS Data Output for Chi^2 test of association between shark behaviour and direction of travel.

Direction * Behaviour Crosstabulation

			Behaviour		Total
			Active	Lethargic	
Direction	With the Current	Count	136	273	409
		Expected Count	108.5	300.5	409.0
	Into the Current	Count	115	422	537
		Expected Count	142.5	394.5	537.0
Total		Count	251	695	946
		Expected Count	251.0	695.0	946.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	16.687[a]	1	.000		
Continuity Correction[b]	16.085	1	.000		
Likelihood Ratio	16.580	1	.000		
Fisher's Exact Test				.000	.000
Linear-by-Linear Association	16.669	1	.000		
N of Valid Cases	946				

a. 0 cells (0.0%) have expected count less than 5. The minimum expected count is 108.52.

b. Computed only for a 2x2 table

Symmetric Measures

		Value	Asymp. Std. Error[a]	Approx. T[b]	Approx. Sig.
Nominal by Nominal	Phi	1.000			.000
	Cramer's V	1.000			.000
	Contingency Coefficient	.707			.000
Ordinal by Ordinal	Kendall's tau-b	.485	.032	-15.983	.000
N of Valid Cases		946			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

Appendix 7

SPSS Data Output for Chi^2 test of association between shark behaviour and remora attachment.

Attachment * Behaviour Crosstabulation

			Behaviour		Total
			Active	Lethargic	
Attachment	With Remora	Count	142	60	202
		Expected Count	47.1	154.9	202.0
	Without Remora	Count	475	1967	2442
		Expected Count	569.9	1872.1	2442.0
Total		Count	617	2027	2644
		Expected Count	617.0	2027.0	2644.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	269.606[a]	1	.000		
Continuity Correction[b]	266.771	1	.000		
Likelihood Ratio	220.871	1	.000		
Fisher's Exact Test				.000	.000
Linear-by-Linear Association	269.504	1	.000		
N of Valid Cases	2644				

a. 0 cells (0.0%) have expected count less than 5. The minimum expected count is 47.14.

b. Computed only for a 2x2 table

Symmetric Measures

		Value	Asymp. Std. Error[a]	Approx. T[b]	Approx. Sig.
Nominal by Nominal	Phi	.036			.000
	Cramer's V	.036			.000
	Contingency Coefficient	.036			.000
Ordinal by Ordinal	Kendall's tau-b	.036	.035	1.022	.042
N of Valid Cases		846			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

Appendix 8

SPSS Data Output for Chi^2 test of association between shark size and:

8.1. Whale shark behaviour.

Behaviour * Size Crosstabulation

			Size			Total
			small	medium	large	
Behaviour	active	Count	77	372	32	481
		Expected Count	63.5	394.4	23.0	481.0
	lethargic	Count	185	1255	63	1503
		Expected Count	198.5	1232.6	72.0	1503.0
Total		Count	262	1627	95	1984
		Expected Count	262.0	1627.0	95.0	1984.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	10.073[a]	2	.006
Likelihood Ratio	9.602	2	.008
Linear-by-Linear Association	.323	1	.570
N of Valid Cases	1984		

Symmetric Measures

		Value	Asymp. Std. Error[a]	Approx. T[b]	Approx. Sig.
Nominal by Nominal	Phi	.069			.009
	Cramer's V	.069			.009
	Contingency Coefficient	.069			.009
Ordinal by Ordinal	Kendall's tau-b	.016	.024	.689	.028
N of Valid Cases		1986			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

8.2. Remora Attachment.

Attachment * Size Crosstabulation

			Size			
			Small	Medium	Large	Total
Attachment	With Remora	Count	33a	128b	4b	165
		Expected Count	21.8	135.3	7.9	165.0
	Without Remora	Count	229a	1499b	91b	1819
		Expected Count	240.2	1491.7	87.1	1819.0
Total		Count	262	1627	95	1984
		Expected Count	262.0	1627.0	95.0	1984.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	8.822[a]	2	.012
Likelihood Ratio	8.472	2	.014
Linear-by-Linear Association	8.728	1	.003
N of Valid Cases	1984		

Symmetric Measures

		Value	Asymp. Std. Error[a]	Approx. T[b]	Approx. Sig.
Nominal by Nominal	Phi	.067			.012
	Cramer's V	.067			.012
	Contingency Coefficient	.066			.012
Ordinal by Ordinal	Kendall's tau-b	.065	.023	2.750	.006
N of Valid Cases		1986			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

Appendix 9

SPSS Data Output for Chi^2 test of association between sea state and:

9.1. Whale shark behaviour.

Crosstab

			Behaviour		Total
			active	lethargic	
seastate	Calm	Count	242	804	1046
		Expected Count	253.8	792.2	1046.0
	Slight	Count	142	430	572
		Expected Count	138.8	433.2	572.0
	Moderate	Count	113	333	446
		Expected Count	108.2	337.8	446.0
	Rough	Count	24	59	83
		Expected Count	20.1	62.9	83.0
Total		Count	521	1626	2147
		Expected Count	521.0	1626.0	2147.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	2.079[a]	3	.556
Likelihood Ratio	2.045	3	.563
Linear-by-Linear Association	1.852	1	.174
N of Valid Cases	2147		

9.2. Remora Attachment.

Crosstab

			Attachment		Total
			with remora	without remora	
seastate	Calm	Count	79	901	980
		Expected Count	98.7	881.3	980.0
	Slight	Count	82	430	512
		Expected Count	51.6	460.4	512.0
	Moderate	Count	20	333	353
		Expected Count	35.6	317.4	353.0
	Rough	Count	12	59	71
		Expected Count	7.2	63.8	71.0
Total		Count	193	1723	1916
		Expected Count	193.0	1723.0	1916.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	35.563[a]	3	.000
Likelihood Ratio	33.870	3	.000
Linear-by-Linear Association	1.417	1	.234
N of Valid Cases	1916		

Symmetric Measures

		Value	Asymp. Std. Error[a]	Approx. T[b]	Approx. Sig.
Nominal by Nominal	Phi	.035			.000
	Cramer's V	.035			.000
	Contingency Coefficient	.034			.000
Ordinal by Ordinal	Kendall's tau-b	.038	.020	-1.866	.062
N of Valid Cases		1906			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

Appendix 10

SPSS Data Output for Chi^2 test of association between season and:

10.1. Whale shark behaviour.

Season * Behaviour Crosstabulation

			Behaviour		Total
			Active	Lethargic	
Season	Dry N.E Monsoon	Count	376	1195	1571
		Expected Count	369.0	1202.0	1571.0
	Wet S.W Monsoon	Count	249	841	1090
		Expected Count	256.0	834.0	1090.0
Total		Count	625	2036	2661
		Expected Count	625.0	2036.0	2661.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	.425[a]	1	.514		
Continuity Correction[b]	.367	1	.545		
Likelihood Ratio	.426	1	.514		
Fisher's Exact Test				.546	.273
Linear-by-Linear Association	.425	1	.514		
N of Valid Cases	2661				

a. 0 cells (0.0%) have expected count less than 5. The minimum expected count is 256.01.

b. Computed only for a 2x2 table

10.2. Remora Attachment.

Season * Attachment Crosstabulation

			Attachment		Total
			Yes	No	
Season	Dry N.E Monsoon	Count	162	1409	1571
		Expected Count	119.8	1451.2	1571.0
	Wet S.W Monsoon	Count	41	1049	1090
		Expected Count	83.2	1006.8	1090.0
Total		Count	203	2458	2661
		Expected Count	203.0	2458.0	2661.0

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	39.184[a]	1	.000		
Continuity Correction[b]	38.260	1	.000		
Likelihood Ratio	42.641	1	.000		
Fisher's Exact Test				.000	.000
Linear-by-Linear Association	39.169	1	.000		
N of Valid Cases	2661				

a. 0 cells (0.0%) have expected count less than 5. The minimum expected count is 83.15.

Symmetric Measures

		Value	Asymp. Std. Error[a]	Approx. T[b]	Approx. Sig.
Nominal by Nominal	Phi	.121			.000
	Cramer's V	.121			.000
	Contingency Coefficient	.120			.000
Ordinal by Ordinal	Kendall's tau-b	.121	.017	6.818	.000
N of Valid Cases		2661			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

Appendix 11

SPSS Data Output for Mann Whitney U test of association between temperature and remora attachment.

Ranks

	Attachment	N	Mean Rank	Sum of Ranks
Temperature	With remora	122	593.94	72460.50
	Without Remora	1117	622.85	695719.50
	Total	1239		

Test Statistics[a]

	Temperature
Mann-Whitney U	64957.500
Wilcoxon W	72460.500
Z	-.891
Asymp. Sig. (2-tailed)	.382

a. Grouping Variable: Attachment

Appendix 12

SPSS Data Output for Mann Whitney U test of association between number of boats and:

12.1. Whale shark behaviour.

Descriptive Statistics

	N	Mean	Std. Deviation	Minimum	Maximum	Percentiles		
						25th	50th (Median)	75th
Boats#	1585	3.45	4.047	0	80	1.00	2.00	5.00
behaviour	1588	1.1474	.35457	1.00	2.00	1.0000	1.0000	1.0000

Ranks

	behaviour	N	Mean Rank	Sum of Ranks
Boats#	lethargic	1352	838.87	1134155.00
	active	233	526.82	122750.00
	Total	1585		

Test Statistics[a]

	Boats#
Mann-Whitney U	95489.000
Wilcoxon W	122750.000
Z	-10.009
Asymp. Sig. (2-tailed)	.000

a. Grouping Variable: behaviour

12.2. Remora Attachment.

Descriptive Statistics

	N	Mean	Std. Deviation	Minimum	Maximum	Percentiles		
						25th	50th (Median)	75th
Boats#	1585	3.45	4.047	0	80	1.00	2.00	5.00
attachment	1588	1.8892	.31402	1.00	2.00	2.0000	2.0000	2.0000

Ranks

	attachment	N	Mean Rank	Sum of Ranks
Boats#	Present	176	560.99	98735.00
	Absent	1409	821.98	1158170.00
	Total	1585		

Test Statistics[a]

	Boats#
Mann-Whitney U	83159.000
Wilcoxon W	98735.000
Z	-7.427
Asymp. Sig. (2-tailed)	.000

a. Grouping Variable: attachment

Appendix 13

SPSS Data Output for Mann Whitney U test of association between number of persons and:

13.1. Whale shark behaviour.

Descriptive Statistics

	N	Mean	Std. Deviation	Minimum	Maximum	Percentiles		
						25th	50th (Median)	75th
people#	1525	21.91	23.254	0	200	6.00	13.00	30.00
behaviour	1525	1.1534	.36053	1.00	2.00	1.0000	1.0000	1.0000

Ranks

	behaviour	N	Mean Rank	Sum of Ranks
people#	lethargic	1291	816.49	1054091.50
	active	234	467.88	109483.50
	Total	1525		

Test Statistics[a]

	people#
Mann-Whitney U	81988.500
Wilcoxon W	109483.500
Z	-11.150
Asymp. Sig. (2-tailed)	.000

a. Grouping Variable: behaviour

13.2. Remora Attachment.

Ranks

	attachment	N	Mean Rank	Sum of Ranks
people#	remora present	160	461.64	73863.00
	remora absent	1365	798.32	1089712.00
	Total	1525		

Test Statistics[a]

	people#
Mann-Whitney U	60983.000
Wilcoxon W	73863.000
Z	-9.156
Asymp. Sig. (2-tailed)	.000

a. Grouping Variable: attachment

Appendix 14

SPSS Data Output for Logistic Regression of temperature on remora attachment likelihood.

Case Processing Summary

Unweighted Cases[a]		N	Percent
Selected Cases	Included in Analysis	1240	100.0
	Missing Cases	0	.0
	Total	1240	100.0
Unselected Cases		0	.0
Total		1240	100.0

a. If weight is in effect, see classification table for the total number of cases.

Classification Table[a,b]

	Observed		Predicted		
			Attchment		Percentage Correct
			Yes	No	
Step 0	Attchment	Yes	0	122	.0
		No	0	1118	100.0
	Overall Percentage				90.2

a. Constant is included in the model.

b. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 0	Constant	2.215	.095	539.803	1	.000	9.164

Model Summary

Step	-2 Log likelihood	Cox & Snell R Square	Nagelkerke R Square
1	795.865[a]	.001	.003

a. Estimation terminated at iteration number 5 because parameter estimates changed by less than .001.

Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	6.452	3	.092

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	1.515	1	.218
	Block	1.515	1	.218
	Model	1.515	1	.218

Variables in the Equation

								95% C.I.for EXP(B)	
		B	S.E.	Wald	df	Sig.	Exp(B)	Lower	Upper
Step 1[a]	Temperature	.125	.102	1.507	1	.220	1.134	.928	1.385
	Constant	1.833	.321	32.604	1	.000	6.255		

a. Variable(s) entered on step 1: Temperature.

Appendix 15

SPSS Data Output for Logistic Regression of number of boats and persons on whale shark behaviour.

Case Processing Summary

Unweighted Cases[a]		N	Percent
Selected Cases	Included in Analysis	1343	50.5
	Missing Cases	1318	49.5
	Total	2661	100.0
Unselected Cases		0	.0
Total		2661	100.0

a. If weight is in effect, see classification table for the total number of cases.

Classification Table[a,b]

	Observed		Predicted		
			behaviour		Percentage Correct
			lethargic	active	
Step 0	behaviour	lethargic	1151	0	100.0
		active	192	0	.0
	Overall Percentage				85.7

a. Constant is included in the model.

b. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 0	Constant	-1.791	.078	527.763	1	.000	.167

Model Summary

Step	-2 Log likelihood	Cox & Snell R Square	Nagelkerke R Square
1	970.999[a]	.093	.166

a. Estimation terminated at iteration number 6 because parameter estimates changed by less than .001.

Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	21.531	8	.006

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	131.085	2	.000
	Block	131.085	2	.000
	Model	131.085	2	.000

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I.for EXP(B)	
								Lower	Upper
Step 1[a]	people	-.048	.007	41.660	1	.000	.953	.940	.967
	boats	-.242	.046	27.611	1	.000	.785	.718	.859
	Constant	-.432	.144	8.965	1	.003	.649		

a. Variable(s) entered on step 1: people, boats.

Correlation Matrix

		Constant	people	boats
Step 1	Constant	1.000	-.518	-.586
	people	-.518	1.000	-.102
	boats	-.586	-.102	1.000

Appendix 16

SPSS Data Output for Logistic Regression of number of boats and persons on remora attachment likelihood.

Case Processing Summary

Unweighted Cases[a]		N	Percent
Selected Cases	Included in Analysis	1343	50.5
	Missing Cases	1318	49.5
	Total	2661	100.0
Unselected Cases		0	.0
Total		2661	100.0

a. If weight is in effect, see classification table for the total number of cases.

Classification Table[a,b]

	Observed		Predicted		
			attachment		Percentage Correct
			remora present	remora absent	
Step 0	attachment	remora present	0	139	.0
		remora absent	0	1204	100.0
	Overall Percentage				89.7

a. Constant is included in the model.

b. The cut value is .500

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)
Step 0	Constant	2.159	.090	580.821	1	.000	8.662

Model Summary

Step	-2 Log likelihood	Cox & Snell R Square	Nagelkerke R Square
1	794.576[a]	.071	.146

a. Estimation terminated at iteration number 7 because parameter estimates changed by less than .001.

Hosmer and Lemeshow Test

Step	Chi-square	df	Sig.
1	18.013	8	.021

Omnibus Tests of Model Coefficients

		Chi-square	df	Sig.
Step 1	Step	99.070	2	.000
	Block	99.070	2	.000
	Model	99.070	2	.000

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I.for EXP(B)	
								Lower	Upper
Step 1[a]	people	.054	.009	33.474	1	.000	1.055	1.036	1.074
	boats	.214	.051	17.482	1	.000	1.239	1.120	1.369
	Constant	.822	.163	25.529	1	.000	2.274		

a. Variable(s) entered on step 1: people, boats.

Correlation Matrix

		Constant	people	boats
Step 1	Constant	1.000	-.523	-.572
	people	-.523	1.000	-.111
	boats	-.572	-.111	1.000

Appendix 17

Risk Assessment.

CHECKLIST FOR SITE VISITS

Organising Department or Faculty		Date of Visit	19.07.2015-16.08.2015
Organisers name:		Contact Details: (mobile/ telephone)	
Name of Site/ Premises:	Maldives Whale Shark Research Programme	Address:	TME Retreats, Adh. Dhigurah, South Ari atoll, Republic of Maldives
Site Contact Name:	Katie Hindle	Site Contact Details: (mobile/ telephone)	00960 7514236
Emergency Contact Details:		1) Richard Rees – 0044 7939 966 539 2) James Hancock – 001 416 303 3225 3) Ibrahim Shameel – 00960 7932446	

Prior to the site visit the following check list should be completed to allow the organiser to assess whether the risks posed by the visit are adequately controlled and that the visit should go ahead.

Not all the questions will apply to all visits, particularly lower risk visits.

Where additional information is required it should be supplied separately to this form.

Appropriate information supplied by the host employer should be passed to people taking part in the visit to ensure that they are aware of the health and safety arrangements and have the appropriate personal protective equipment, clothing and equipment.

No.		Yes	No	N/A
1	Does the host employer have appropriate public liability insurance?	X		
2	Does the host employer have a health and safety policy outlining their arrangements for health and safety?	X		
3	Has the host employer undertaken risk assessments in relation to visitors to their site/premises?	X		
4	Are there fire, emergency and evacuation procedures in place together with arrangements for sharing this information with visitors?	X		

5	Are there arrangements for visitors to the site to receive an induction from the host employer?	X		
6	Are there arrangements for the visitors to be supervised by the host employer whilst on site?	X		
7	Are first aid arrangements in place?	X		
6	Are arrangements in place to ensure that visitors have the appropriate personal protective equipment, clothing, footwear and equipment? Please specify.			X
7	If visitors will be using any work equipment are arrangements in place for them to receive appropriate training?			X
8	If the University has organised transport to the site, has this been provided by an approved supplier?			X
9	Are there any other significant risks associated with the site/premises e.g. uneven ground, falls from height, risks from vehicles, poor lighting? Please specify	X		
10	Is the visit accessible for people with disabilities?		X	
11	Are there any other risks associated with the site/premises of which visitors should be aware? Please specify In conjunction to the additional information required highlighted in Question 9, the MWSRP has identified risks associated with operating at sea from a research vessel in a tropical, remote climate. A full risk assessment and mitigating measures employed by the organisation, as well as other notes on safety in country has been attached to this form. The MWSRP remain available for contact should any further clarifications be required in this regard. .			

Signature **Richard Rees**	Date 29.05.2015