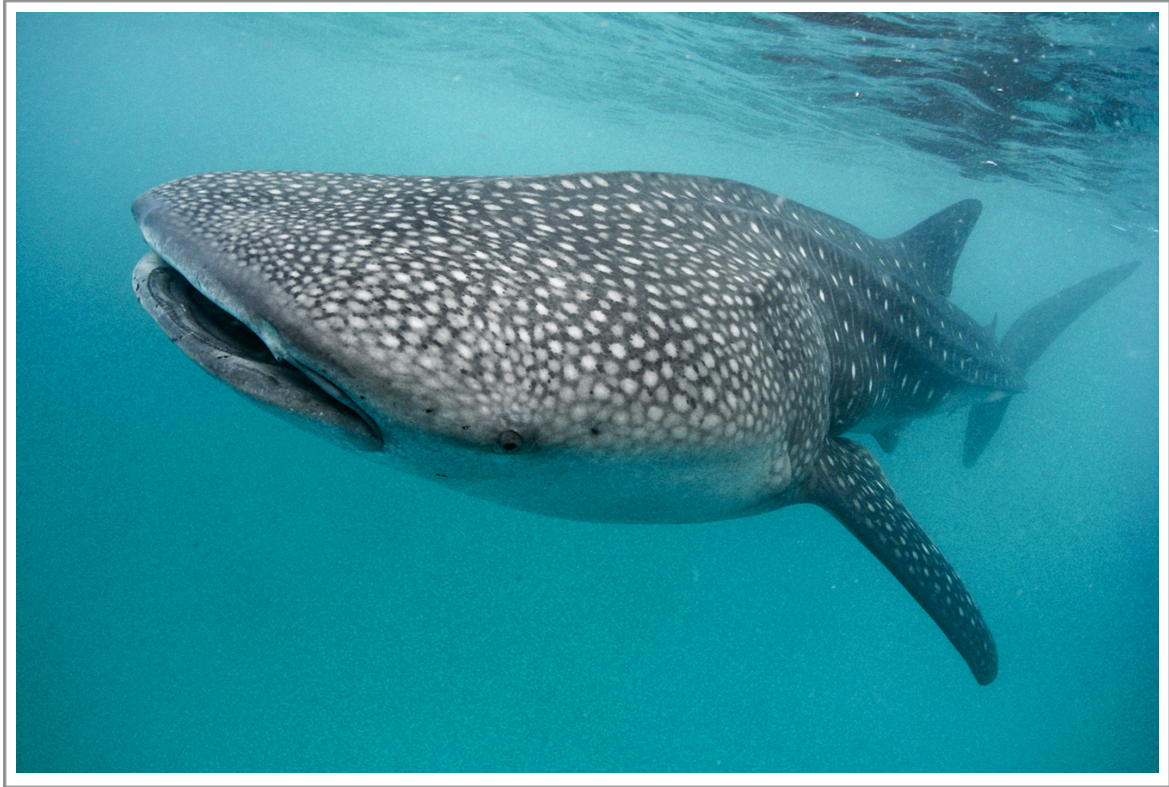


**An assessment of the conservation status of the
whale shark *Rhincodon typus* in the Republic of
Maldives using photo-identification and mark-
recapture techniques**

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*A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science and the Diploma of Imperial College London*



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*“What is the answer to the Great Question of Life, the Universe and Everything?
Forty-two” said Deep Thought, with infinite majesty and calm.*

(Douglas Adams, The Hitchhiker’s Guide To The Galaxy, 1978)

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Abstract

The whale shark is the largest and one of the most well known of all shark species, yet despite this its conservation status remains ambiguous. Over the past decade only a handful of whale shark aggregations have received any research attention, and information from these studies guides whale shark conservation management throughout the rest of their range. This study is the first to investigate the conservation status and population ecology of whale sharks in the Maldives in an attempt to generate locally relevant ecological information and meliorate national conservation management.

Whale shark life history traits are investigated using a combination of mark-recapture techniques and photo-identification, with data of varying quality collected from a wide range of sources. The suitability of using such a variety of data with mark-recapture studies is discussed, concluding that although quality of data can influence parameter estimates if not accounted for, in general data sourced from non-experts allows for the accurate estimation of demographic parameters.

Mark-recapture analysis reveals that the Maldivian whale shark population is distinct from other studied whale shark aggregations, with individuals demonstrating high survival rates and prolonged residency within key areas. Population size and growth rate were estimated for a six year period, and show no compelling evidence for a decline in the population. Furthermore, there is some evidence to suggest that loss from the population is driven by emigration of maturing individuals rather than mortality.

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This study represents a joint effort by several individuals, all of whom share a common goal, namely the conservation of whale sharks in the Maldives.

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1.0 INTRODUCTION

The investigation of ecological and demographic parameters is central to conservation biology, with estimates of abundance and apparent survival rate, as well as geographic distribution and movement used to inform conservation management decisions.

For many species, especially those of commercial importance, estimates of abundance and related life-history traits can be gleaned from off-take data (e.g. Ichii et al, 2006; Myers, 2007). However, data from harvesting activities may not be available, or indeed appropriate, for many rare or commercially unimportant species. In this situation mark-recapture methods provide a much less intrusive, and more sustainable, alternative.

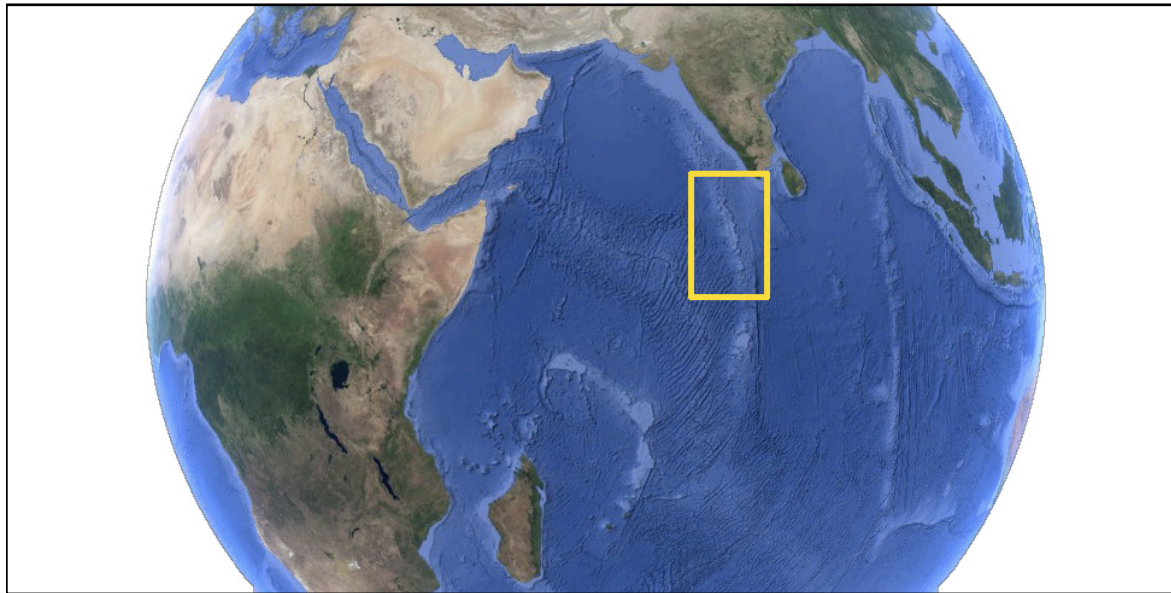
Over the past 100 years mark-recapture has most commonly been used to estimate the size of wildlife populations. More recently however, with the persistent development of newer and more sophisticated models, many studies have shifted their focus towards the estimation of a range of other demographic parameters, such as survival, recruitment and fecundity rates (Williams et al, 2001).

1.1 Research focus

The whale shark *Rhincodon typus* is a large, relatively uncommon species (Compagno, 2001), and although still commercially exploited some areas, fisheries data are sparse due to the poor reporting of catches (Camhi et al, 2009). As a result whale sharks have become been the focus of several recent mark-recapture studies (Meekan et al, 2006; Bradshaw et al, 2007; Graham & Roberts, 2007; Holmberg et al, 2008, 2009), and appear to be well suited to such an approach.

The Republic of Maldives is a string of coral atolls and small islands, straddling the equator southwest of India (Picture 1.1). The archipelago, which boasts a diverse catalogue of megafauna, is a range state of the whale shark (Anderson & Ahmed, 1993; Rowat, 2007). This large and charismatic species features

prominently in the county's ecotourism industry, yet until recently there have been no firm attempts to study the population, and consequently very little is known about population size, demographic parameters, movement or conservation status.



Picture 1.1 A view of the Earth from space showing the position of the Maldives (yellow rectangle) (Picture © Google Earth 2009)

1.2 Relevance of the study

Biodiversity underpins the majority of economic activity in the Maldives, and the country relies heavily on its ever expanding tourism industry with this sector alone contributing 34% of national GDP (Emerton et al, 2009). Traditional fishing and shipping industries have been overtaken by tourism, which centers itself around the archipelago's favourable location and natural beauty, and consequently there has been a shift away from extractive exploitation of natural resources towards improved stewardship of the natural environment. An example of this can be seen through a number of conservation policies introduced over the past 20 years which have resulted in the legal protection of several species, including the 1995 suspension of the national whale shark fishery.

In 2002, under its commitments to the Convention on Biological Diversity, the Maldivian government produced a National Biodiversity Strategy and Action Plan (Jameel et al, 2002), and more recently has announced the creation of three new Marine Protected Areas (MPA) (AEC, 2009), demonstrating its commitment to safeguarding national biodiversity. One of these newly designated MPA areas, Hanifaru in Baa Atoll, was awarded protection based on its importance as a seasonal feeding site for both whale sharks and manta rays *Manta birostris*. In addition, an MPA in South Ari Atoll is currently in the consultation stage and is expected to be gazetted in 2010 (A. Harman & R. Rees; personal communication), again due to its importance as an aggregation site for whale sharks. However, without sound ecological knowledge of the Maldivian whale shark population, the success of any targeted conservation management will be limited.

1.3 Aims and objectives

With the conservation status of the Maldivian whale shark population as yet undetermined, this study aims to employ mark-recapture techniques to elucidate the key life-history traits which underpin local population dynamics. The outputs can be used to inform conservation management of the species, and to facilitate future monitoring activities.

The study has several objectives;

- ▶ **To explore the suitability of mark-recapture techniques using data collected from both expert and non-expert sources.** Mark-recapture models have underlying assumptions which must be met to enable accurate estimation of demographic parameters, and so the ability of the data to meet these assumptions will be investigated.
- ▶ **To report on the geographic and temporal distribution of whale sharks throughout the archipelago.** The Maldives is known to support a year round population of whale sharks, although it is not fully understood how this population is distributed through space and time.
- ▶ **To estimate the population size and apparent survival rate at a key whale shark aggregation site within the Maldives.** These parameters, which can be estimated using mark-recapture methods, are essential for effective and ongoing conservation management of the population.
- ▶ **To investigate changes in abundance over a six year period.** The change in size of the population over this time scale, either positive or negative, will provide the first indication of the short-term conservation status of the Maldivian whale shark population.

2.0 BACKGROUND

2.1 Population ecology

Wild populations are not static, but are instead moulded and reshaped over time in response to natural and anthropogenic forces acting upon them. It stands to reason then that if species are to be managed and conserved at the population level, the demographic cogs driving population dynamics must be investigated and understood.

Population abundance refers to the size of the population at a particular time, and is perhaps the most commonly studied of all population characteristics. In fisheries management, population size is an essential piece of information when determining catch quotas or introducing harvesting restrictions, and fish stocks are constantly re-assessed to provide up-to-date abundance estimates (Gayanilo et al, 2005). In a similar vein, the IUCN Red List uses estimates of population size as a criterion when making broad assessments of a species' conservation status (IUCN, 2001), and local conservation projects often track abundance over time as part of on-going monitoring activity (Milner-Gulland & Rowcliffe, 2007).

There are three major sampling methods commonly used to estimate abundance; distance sampling, offtake-based sampling and mark-recapture sampling. Distance sampling is best suited to easy-to-see species, and typically involves counting individuals along a transect and noting their distance from the line to calculate a detection function. This allows estimation of both the observed and unobserved proportions of the population, from which total abundance can be inferred (Milner-Gulland & Rowcliffe, 2007). However, the use of distance sampling is restricted in many habitats, such as dense forest and marine environments where visibility is reduced.

Offtake-based sampling is most commonly applied to data taken from extractive industries, such as commercial fisheries, where abundance can be estimated and

monitored through statistics such as catch per unit effort (Milner-Gulland & Rowcliffe, 2007). Many high priority conservation assessments which focus on marine species must rely almost exclusively on data from off-take (e.g. IUCN report on the Conservation Status of Pelagic Sharks and Rays; Camhi et al, 2009) due to the difficulty associated with studying remote populations of highly mobile species.

2.2.1 Introduction to mark-recapture

Mark-recapture sampling is a versatile technique which, in addition to the estimation of abundance, opens up an almost overwhelming number of possibilities in the investigation of demographic parameters (Williams et al, 2001). The underlying method involves the initial capture and marking of a sample of animals from a population, followed by a minimum of one recapture event where the population is again sampled. In the most basic mark-recapture experiments animals need only be given a generic mark, identifying them in later samples as having been previously caught. However, in more sophisticated mark-recapture studies individuals are distinguished from one another, either through an artificially applied mark or by some virtue of their physical appearance.

Marking techniques vary in how invasive they are, and include the use of paints and dyes, tags, mutilation and genetic marking (Olsen, 2006). One of the least invasive methods of marking is photo-identification, which has been used successfully for some time with cetaceans (Hammond et al, 1990), cheetahs (Kelly, 2001), tigers (Karanth, 2005), manatees (Langtimm et al, 2004) and several species of shark (e.g. Van Tienhoven et al, 2007; Speed et al, 2007).

2.2.2 Marking with photo-identification

Individuals of many species have a unique pattern or physical idiosyncrasy from which they can be identified. Photography of these identifying characteristics creates a visual record - in effect a virtual tag - which can be used to match

individuals within a reference library. Furthermore, this process of marking individuals, which may require equipment no more sophisticated than a camera, is often a much cheaper and less intrusive alternative to conventional tagging. A large volume of images can be compiled to create a photo-identification catalogue, providing opportunity for mark-recapture analysis (e.g. The Dolphin Project, Lapolla, 2005; SPLASH, Calambokidis et al, 2008).

Research projects which employ photo-identification often use images taken by trained observers, but in theory photographs can come from many other non-specialist sources, increasing the applicability of the method. The widespread use of underwater cameras by tourists visiting Ningaloo Reef in Western Australia has enabled researchers to collect a large volume of photographic data documenting the annual whale shark aggregation (Meekan et al, 2006; Holmberg et al, 2008, 2009). Whale sharks are highly suited to visual identification with each shark having a unique and immutable pattern of lines and spots (Arzoumanian et al, 2005; Meekan et al, 2006), and the universal popularity of whale shark tourism has resulted in photographic data becoming available for many aggregations worldwide. As a result, two comprehensive online catalogues have been established (ECOCEAN Whale Shark Photo-Identification Library, www.whaleshark.org; Shark Trust Whale Shark Project, www.whalesharkproject.org) which act as repositories for global whale shark sightings, facilitating both individual and collaborative research efforts.

Although individuals can be matched from photographs visually, relying on eyesight alone becomes inefficient and unreliable as the size of the reference catalogue increases (Speed et al, 2007). To aid in the identification and matching process, several computer software programs have been developed which employ powerful algorithms to rapidly scan through hundreds of images. Two such software programs are available for use with whale sharks. One, utilised by the ECOCEAN Whale Shark Photo-Identification Library (although not publicly

available), employs a computer algorithm initially designed for matching celestial patterns in the night sky (Arzoumanian et al, 2005). The second, which is freely available for download over the internet (www.reijns.com/i3s), can also be applied to pattern-matching of the spotted ragged-tooth shark *Carcharias taurus* and the manta ray (Van Tienhoven et al, 2007).

2.2.3 The theory behind mark-recapture models

A huge number of different models are available to estimate various ecological and demographic parameters from mark-recapture experiments, but all use the same data format and follow the same basic data collection protocol:

A sample of animals from a population are caught during a capture event, marked in some way, and then released back into the population where they mix with unmarked animals. After a reasonable time period, the population is revisited and re-sampled, with the newly captured sample now being made up of both unmarked and previously marked animals. The process is repeated several times, with unmarked animals given a mark before being returned to the population each time. The terms 'capture' and 'recapture' in this sense are quite broad, and can simply involve sightings and re-sightings if a non-invasive method of marking, such as photo-identification, is used.

Eventually the outcome of each capture event can be strung together to generate a capture history for each individual marked in the study, with 1s indicating that the individual was captured, and 0s indicating that it was not, e.g.;

1 0 0 1 1 0 0 0 0 1

In this example, which represents a series of ten capture sessions, the individual was initially capture in session one, and subsequently recaptured in sessions four, five and ten.

Whether or not an individual is captured depends not only on it being alive and in the study population, but also on its chance of capture. More formally this is described as the probability of survival (ϕ) and the probability of capture (p). In fact, in this situation, 'survival' is more accurately termed 'apparent survival', as mortality and permanent emigration, which would both result in an individual being permanently unavailable for capture, cannot be distinguished from one another in this simplified format.

The Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) is one of the most basic mark-recapture models, and is used to estimate values for ϕ_i and p_i - where i represents a particular time period - using the process of maximum likelihood estimation, which can be broken down into two steps. The first involves describing the probability of each capture (1) or non-capture (0) occurring at each capture event, then building these up to describe the entire capture history in probability terms, e.g.;

$$\begin{array}{ccc|l} 1 & 1 & 0 & P = \phi_1 p_2 [\phi_2 (1 - p_3) + (1 - \phi_2)] \\ 1 & 0 & 1 & P = \phi_1 (1 - p_2) \phi_2 p_3 \end{array}$$

If p is the probability of an individual being captured, then the probability of it not being captured is $(1 - p)$, and the same applies to apparent survival. In the above example, the first capture history shows that the animal was captured in the first capture session, was alive and recaptured in the second session ($\phi_1 p_2$), and either survived to the final session but was not caught ($\phi_2 (1 - p_3)$), or had permanently left the population or died ($1 - \phi_2$). In the second example the animal was again caught in the first capture session, survived into the next session but was not captured ($\phi_1 (1 - p_2)$), and was recaptured in the final session ($\phi_2 p_3$).

Therefore, because a capture history can be explained by a series of survival and capture probabilities, the likelihood of that particular capture history occurring (P) is simply the product of these probabilities. Following this logic, the likelihood of

all of the capture histories occurring (L) is a product of all P probabilities. This introduces the second step in maximum likelihood estimation, which involves finding the values of p_i and ϕ_i which maximise the overall likelihood of the observed capture histories occurring. Put another way, the process of maximum likelihood involves making constant and judicious changes to the values of apparent survival and capture probability until values are found which best explain the actual pattern of captures observed during the study.

Although the CJS approach can be used as a stand alone model, it also forms the foundation for more sophisticated mark-recapture models. These more complex models, which can be used to estimate additional ecological parameters such as abundance, population growth rate and recruitment (Amstrup et al, 2005; Cooch & White, 2006), also use the method of maximum likelihood estimation, with the parameter of interest included within the likelihood function.

2.3 A review of whale shark biology and ecology

Widely quoted as being the planet's largest fish, the whale shark reaches lengths of 10-12m, with some reports exceeding 18m (Compagno, 2001; Stewart & Wilson, 2005). By virtue of its enormity, aesthetics and passive nature, the whale shark proves to be a popular species with tourists and fuels lucrative ecotourism industries in several countries throughout its range (Graham, 2007; Jones et al, 2009). Yet despite this public attention surprisingly little is known about many of the whale shark's basic biological and ecological characteristics.

First described by Andrew Smith from an individual harpooned off the South African coast in 1828, the species has remained elusive and enigmatic until quite recently. During the century following its taxonomic discovery, publications focused mainly on distribution, with life history traits left to conjecture (Stevens, 2007). Only since the 1980s has research slowly begun to unravel the biology of the whale shark, although large knowledge gaps still exist. In 2000, Fowler produced a

review of current whale shark knowledge, highlighting the paucity of information available, which has served to direct a flurry of studies over the last decade. The majority of these recent studies have focused on tracking the movement of whale sharks, and on elucidating key aspects of population ecology using mark-recapture techniques (Martin, 2007; Stevens, 2007).

Tagging studies have dramatically improved our understanding of whale shark movement and migration behaviour, and shown the species to be capable of traveling huge distances. Eckert and Stewart (2001) used satellite tags to track whale sharks in the Sea of Cortez and North Pacific. Most of the tagged individuals retained their tags between 12-39 days and dispersed throughout the Sea of Cortez, with several moving out into the North Pacific. One individual, which retained its tag for 37 months, crossed into the Western Pacific, a journey of 13,000 km. In another study by Eckert et al (2002), two sharks tagged in the Sulu Sea travelled 4,567 km and 8,025 km respectively, moving through multiple political jurisdictions and exemplifying the species' cosmopolitan nature.

The individuals tagged by Eckert and Stewart (2001) were recorded diving to depths of 240 m, although much deeper dives have been observed. Brunnschweiler et al (2009) report the movement of a female whale shark tagged off the Mozambique coast making a journey of 1,200 km to the southern coast of Madagascar. During this 87 day journey the shark made multiple dives down through the mesopelagic and bathypelagic zones, on one dive reaching a maximum depth of at least 1,286 m. The reason for these deep dives is not fully understood, but one theory is that a series of deep dives forms a foraging strategy, with the shark searching through several water layers for olfactory clues to the occurrence of zooplankton (Brunnschweiler et al, 2009).

The whale shark's propensity for long distance migration lends some support to the findings of a recent study by Schmidt et al (2009), who have revealed low levels of genetic differentiation between geographically distinct whale shark

populations, suggesting global gene flow. However, it is unclear if this genetic mixing is the result of individuals moving large distances to breed with distant populations, or of sharks breeding with neighbouring populations and subsequent generations again breeding in yet more distant populations.

Although whale sharks are known to undertake trans-oceanic journeys, most satellite tracking studies show sharks moving within their oceanic region (Rowat & Gore, 2007; Graham & Roberts, 2007, Hsu et al, 2007). Whale sharks tagged in Belize travelled exclusively within Central American waters (Graham & Roberts, 2007), and sharks have been tracked traveling northwards up the South African coast from Kwa-Zulu Natal (Gifford et al, 2007). The northeasterly movement of sharks away from Ningaloo Reef in Western Australia (Wilson et al, 2006), along with knowledge gained from photo-identification studies confirming that individuals return to the Ningaloo area on an annual basis (Meekan et al, 2006; Holmberg et al, 2008), suggests that whale sharks undertake short-distance migrations to and from season aggregation sites (Wilson et al, 2006). Further evidence of regional fidelity is provided by Holmberg et al (2008, 2009) who report that of 1,275 sharks photographically tagged off Australia, Christmas Island, the Maldives, Mozambique, the Philippines, the Seychelles and Thailand, only three individuals have been sighted in more than one area.

Predictable whale shark aggregations occur in several coastal areas including Belize (Heyman et al, 2001; Graham & Roberts, 2007), Western Australia (Taylor, 1994, 1996), the Sea of Cortez (Eckert and Stewart, 2001; Nelson, 2004), the Seychelles (Rowat & Gore, 2007), KwaZulu-Natal (Beckley et al, 1997), Kenya, the Galapagos, India (Vivekanandan & Zala, 1994), Mexico and the Maldives, and have become the focus for the most of the recent studies of whale shark ecology and biology. The timing of these aggregations co-insides with seasonal abundance of food, such as spawning of cubera snappers *Lutjanus cyanopterus* and dog snappers *L. jocu* in Belize (Heyman et al , 2001), schools of euphausiids and

baitfish in Western Australia (Taylor 1994, 2007) and zooplankton in the Sea of Cortez (Clarke & Nelson, 1997) and the Gulf of Tadjoura (Rowat et al, 2007).

Typically these aggregations last for up to several months, and whale sharks, which are typically solitary, become functionally gregarious (Stewart & Wilson, 2005). The arrival of whale sharks at the Ningaloo Reef aggregation is staggered, and Holmberg et al (2009) have estimated a residency time of 33 days for participating sharks. The occurrence of whale sharks in Mozambique and Madagascar is reported to be more sustained, with sightings reported throughout the year (Jonahson & Harding, 2007; Brunnschweiler et al, 2009). These populations however have received much less research attention, and very little information has been published in the primary literature as to the number of sharks present and what biological or oceanographic factors sustain such year-round aggregations.

Several other populations have received much greater research attention, and consequently much more is known about their characteristics. Gladden Split in Belize hosts an annual convergence of whale sharks between April and May, which time their arrival to a spawning event (Heyman et al, 2001). Graham and Roberts (2007) report a mean length of 6.3 m total length (TL) from this area, and of 162 sharks sexed 86% were male. Similar observations made at Ningaloo Reef (Taylor, 1994; Meekan et al, 2006), India (Pravin, 2000) the Gulf of Tadjoura (Rowat et al, 2007), the Gulf of California (Eckert & Stewart, 2001) and Thailand (Theberge & Dearden, 2006) suggests that whale sharks segregate by both size and sex, a phenomenon seen in several other species sharks (Bres, 1993).

The age at which whale sharks reach maturity is still largely based on conjecture, with few reliable data available. Norman and Stevens (2007) have used underwater observations of whale sharks at Ningaloo Reef to suggest maturity in males is first reached at ~8 m TL, with 95% of male sharks mature by the time they are ~9 m TL. Sexual maturity in females cannot be determined by observation

alone, and a lack of large females in the study did not allow predictions of maturity length to be made. However, several females below 9m TL have been examined, and all were found to be immature (Pai et al, 1983; Rao, 1986; Beckley et al, 1997). In fact, the only information on a mature female comes from a 10.6 m TL shark fished off Taiwan in 1995, which was pregnant and contained around 300 embryos in various stages of development (Joung et al, 1996). Given this data, Norman and Stevens (2007) suggest that female whale sharks reach maturity at around or above the length reported for males.

The information available on sexual maturity therefore implies that sharks participating in most seasonal aggregations are immature (Schmidt et al, 2009), and in fact large concentrations of mature females have only been reported from the Gulf of California (Nelson & Eckert, 2007) and the Galapagos Islands (Schmidt et al, 2009).

2.4 Current whale shark conservation status

Traditionally the hunting of whale sharks for their meat and oil-rich livers was widespread, but although the demand for these products has fallen several countries continue exploit whale sharks for their valuable fins. Elsewhere the species receives sanctuary, with several countries affording national protection; Australia (1999), Belize (2000), Honduras (1999), India, the Maldives (1995), the Philippines (1998) and the USA (Norman, 2000; Chen & Phipps, 2004).

With evidence for declining catches from the India, the Philippines and Taiwan over the past 10-15 years (Chen & Phipps, 2004) the whale shark is listed as Vulnerable in the IUCN Red List of Threatened Species, and appears on Appendix II of the Convention of Migratory Species, Appendix II of Convention on International Trade in Endangered Species and Annex I of United Nations Convention on the Law of the Sea.

Like most elasmobranchs, whale sharks have slow growth rates and reach sexual maturity late, making them particularly vulnerable to overfishing. A handful of recent studies have used sightings records, aerial surveys and mark-recapture techniques to investigate the trend of several populations, and although there is disagreement in some areas, there is indication that whale sharks are decreasing in number in various regions (Schmidt et al, 2009).

Theberge and Dearden (2006) used sightings data collected by tour operators in Thailand over a 10- year period to report a decline in abundance of 96% between 1992 and 2002. Whale sharks are apparently unfished in Thai waters, and this decline may result from legal or illegal fisheries operating in neighbouring countries. Bradshaw et al (2008) used similar data collected by tour operators at Ningaloo including data on shark length, which showed that mean TL decreased by almost 2 m over a decade; a diagnostic characteristic of commercial exploitation.

An earlier study by Bradshaw et al (2007) used mark-recapture techniques in an attempt to predict the population trajectory at Ningaloo Reef. Population growth rate estimates varied between 0.87 yr^{-1} to 1.26 yr^{-1} , with different models incorporating different biological assumptions - the majority of which reported a decline in the returning Ningaloo whale shark population. Australia offers some of the strongest protection to whale sharks, and observed declines in the population are likely to result from foreign fisheries or illegal hunting throughout Southeast Asia (Bradshaw et al, 2008).

However, the decline in abundance reported in the Ningaloo population has been questioned by some authors. Holmberg et al (2008, 2009) have also employed mark-recapture techniques on the same population and found no evidence of a decline, with two separate models estimating population growth rate at 1.12 yr^{-1} and 1.07 yr^{-1} . The contradiction in these results may be partially explained by the temporal and spatial coverage of the studies, or of the models and techniques

used, but above all it illustrates the ambiguity in our understand of the conservation status of the whale shark, and highlights the need for continued research effort in other regions.

3.0 METHODS

3.1 Data collection

Photographic encounters with whale sharks were submitted from two main sources; non-experts (tourists and resort staff), and experts (researchers). Non-expert submissions were collected both in real-time, through direct correspondence between April and January 2008, and from photographic archives. Several individuals made their personal photographic and video archives available, although the majority of non-expert sightings were sourced from the internet. The online ECOCEAN Whale Shark Photo-identification Library provided a wealth of encounter data, with encounter images and relevant information archived together. In addition, two popular and freely accessible photo-sharing websites, Flickr (www.flickr.com) and YouTube (www.youtube.com), were periodically searched for images of Maldivian whale shark encounters. The contributors were then contacted and asked to verify the encounter and supply further information.

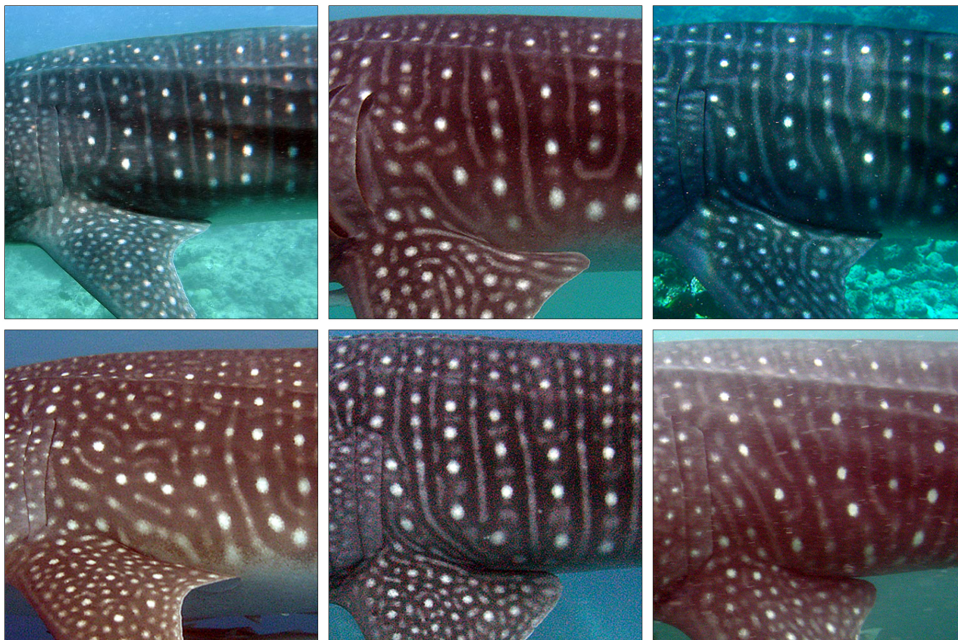
Encounter information generally included the time and date of the sighting along with the approximate location. This was typically given as the nearest reef or tourist resort. In addition, some reports included supplementary information on estimated total length and sex, plus notes on observed behaviour (feeding or cruising) and distinguishing physical features.

Observations made by non-experts are prone to error, especially sex discrimination and estimation of total length (personal observation). Therefore, unless non-expert submissions included photographic evidence for the presence or absence of pelvic claspers then gender was not assigned to a shark. Similarly, length estimates were treated with caution unless a submission included a point of reference, such as a swimmer, diver or boat photographed alongside the shark.

Expert sources included the author, marine biologists and an ephemeral research team conducting whale shark research. Submissions from these sources tended to include more detailed and accurate information, and as a result could be used to confirm or reject observations made by non-experts. Gender was validated, and further visual examination of male pelvic claspers was carried out to gauge the maturity status of the shark. Expert submissions also included accurate length data for some individuals, with measurements of total length made using a tape measure during in-water encounters.

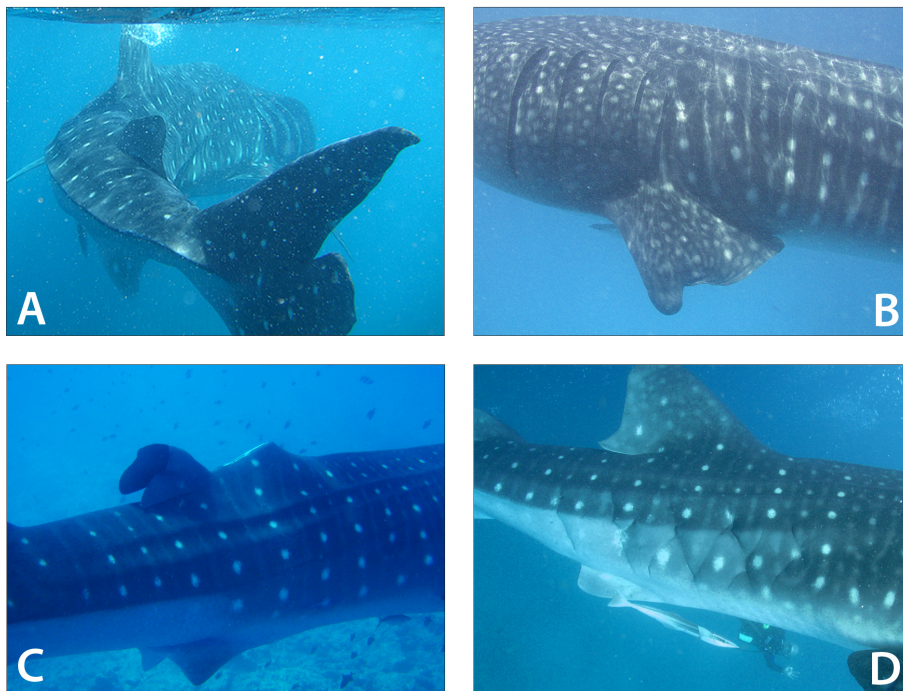
3.2 The photo-identification process

Submissions containing suitable quality visual information, either in the form of photographs or video stills, allowed for the identification of individual sharks and facilitated subsequent mark-recapture analysis. The freely distributed computer software I3S (Interactive Individual Identification Software) was used to assign unique fingerprint-style identities to sharks, and to facilitate the matching of spot patterns within the photo-library.



Picture 3.1 Examples of variation in spot patterns within the region used for photo-identification (Photos © MWSRP & T. Davies).

I3S requires images showing the area directly behind the gills and above the pectoral fin on either side of the shark (Picture 3.1), from which a computer user maps out a minimum of twelve spots falling between three reference points. Although both left- and right-hand side images can be used to match a shark within the photo-library, only left-hand side images were used for the initial identification and cataloguing to prevent allocation of double identities. Once a new fingerprint was mapped, I3S scanned all other fingerprinted images in the photo-library for a match, with potential matches assigned an information criterion weight. If no match was found for a left-hand side fingerprint the entire photo-library was scanned visually before the shark was considered 'new'. New sharks were subsequently assigned an alpha-numeric identification code, and added to the I3S photo-library. If right-hand side images did not yield a match, no identity was created and instead the image was archived for later matching attempts.



Picture 3.2 Examples of obvious physical scarring which can be used in photo-identification; caudal fin (A); pectoral fins (B); dorsal fin (C); and caudal peduncle (D) (Photos © MWSRP & T. Davies).

Spot matching with I3S is restricted by the angle and position of the shark in the image, as well as image quality. Accuracy becomes poor when the horizontal yaw angle of the shark exceeds 30° (Speed et al, 2007), and also when the spot pattern cannot be clearly distinguished due to poor image quality, bad light or murky conditions. When images were unsuitable for I3S, identification was done using visual matching. In addition to spot patterns, images often showed clear identifiable physical features, such as scarring to the body or partial amputations of fins (Picture 3.2), which could be used to match individuals. However, if images gave no clue to identity then the encounter was excluded from mark-recapture analysis.

3.3 Population modelling

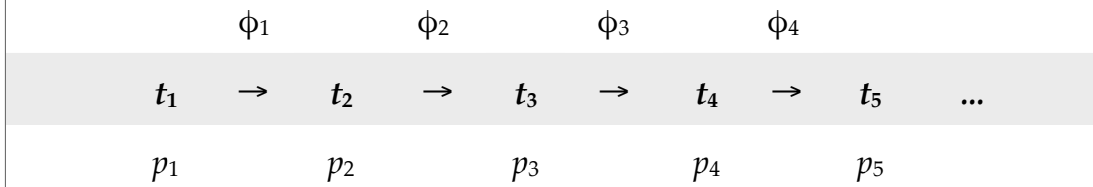
Traditional mark-recapture models require that captures are made during discreet capture sessions, or 'primary periods'. The opportunistic encounter data in this study were effectively collected in continuous time (i.e. encounters did not naturally occur within defined intervals), and so it was necessary to artificially pool data into discreet periods. A compromise was made between ensuring each capture session contained enough data for modelling purposes, and minimising potential bias introduced from extended capture periods, and as a result encounters were pooled into three month periods (quarters).

To choose which family of model to employ, the dynamics of the population first needed to be classed as either open or closed. If the population is considered open, population size and structure are both subject to change between capture sessions through a combination of births, deaths, immigration or emigration. Although evidence of open dynamics is often intuitive from the time scale of the study and the ecology of the study species, statistical tests exist to accept or reject a hypothesis of population closure, allowing selection of the most appropriate model according to the data. The first test, designed by Stanley & Burnham (1999), tests a null hypothesis of population closure against an alternative hypothesis of

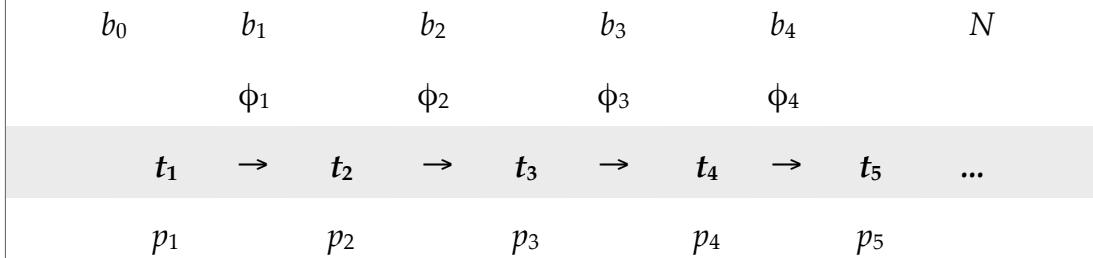
an open population using a chi-squared test. The second test, introduced by Otis et al. (1978), looks at the time interval between initial and final capture to either support or reject a null hypothesis of population closure.

Figure 3.1 Conceptualised time-dependent models for the (a) Cormack-Jolly-Seber approach, (b) POPAN Jolly-Seber formulation, and (c) Pradel- λ Jolly-Seber formulation. In all models, p_i is probability of capture during capture session i , and ϕ_i is the probability of an individual surviving between capture sessions i and $i+1$. For the POPAN formulation, b_i is the probability that a shark from the hypothetical superpopulation (N) enters the studied population during capture session i . In the Pradel- λ formulation, λ_i denotes the rate of population change. Modified from Cooch & White (2006).

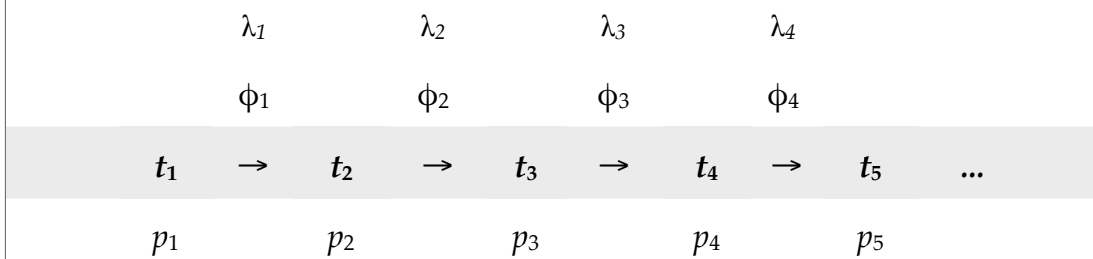
a) Cormack-Jolly-Seber model



b) POPAN Jolly-Seber model



c) Pradel- λ Jolly-Seber model



3.3.1 Estimating apparent survival

The population was found to be open, and consequently open population models were used for all further mark-recapture analysis using the program MARK (White & Burnham, 1999). The Cormack-Jolly-Seber model was used to estimate capture probability (p_i), which is the probability that a marked animal is recaptured during capture session i , and apparent survival (ϕ_i), which is the probability that a shark has not died or permanently emigrated from the population between capture sessions i and $i+1$ (Figure 3.1). The CJS model conditions on marked individuals and only uses recaptures to estimate parameters. Consequently estimates of capture probability and apparent survival apply only to the marked component of the population.

3.3.2 Model Assumptions

A number of key assumptions must be met when applying the CJS modelling approach, the violation of which can lead to either upward or downward bias in the estimation of p_i and ϕ_i (Williams et al, 2001). In the context of this study, these assumptions are:

1. Every marked shark present in the study population and available for capture during capture session i has the same probability of being captured.
2. Every marked shark in the population immediately after capture session i has the same probability of remaining in the population until capture session $i+1$.
3. Identifying marks (i.e. spot patterns) are neither lost nor misinterpreted.
4. Sampling periods are instantaneous relative to the interval between capture sessions.
5. Apparent survival and capture probabilities of each shark are independent of the fate of other sharks.

Heterogeneity in apparent survival and capture probability between individual sharks may be an inevitable result of imperfect study design, especially when using opportunistic data collected from a range of sources (Holmberg et al, 2008, 2009). The implications of opportunistic data collection on model outputs are considered later in detail (see *Discussion*).

The ability of the data to meet the first two assumptions (i.e. goodness of fit) was investigated using Test2 and Test3 (Burnham et al, 1987) in the program U-CARE (Choquet et al, 2005). Test2 is used to reveal significant heterogeneity in capture probability between individuals by testing whether an individual's capture probability is dependent on when that animal was first caught. Furthermore, Test2, which is available as two subtests, Test2.CL and Test2.CT, can define a statistic (z) for 'trap happiness' ($z < 0$) or 'trap shyness' ($z > 0$). In a similar fashion, Test3 detects significant heterogeneity in apparent survival probability. The subtest Test3.SR can be used to define a statistic (z) for transience, which in this context would indicate a large proportion of sharks are encountered in a single capture session ($z > 0$).

Assumption 3 requires that marks are not lost, missed or incorrectly read. Photo-identification provides a virtual tag which cannot easily be lost, and crucially the spot pattern of a whale shark remains static over time (Arzoumanian et al, 2005; Meekan et al, 2006). Misinterpretation of spot patterns is minimised by using a combination of experienced observers and semi-automated photo-identification software (Speed et al, 2007), although mis- or non-identification of individuals can lead to bias in model estimates (see *Discussion*).

Assumption 4 relates to the fact that mark-recapture models assume no death within capture periods, and therefore requires that sampling is effectively instantaneous. Lengthy capture periods potentially introduce bias associated with heterogeneity in apparent survival (Williams et al, 2001), as an animal caught at the end of a long capture period has a greater survival probability than an animal

caught at the beginning, which must also survive the duration of the capture period. However, a contradictory study by O'Brian et al (2005) found that where capture periods were extended to increase sample size, and the assumption of instantaneous sampling was violated, model estimates of apparent survival rate were actually more accurate. The quarterly capture sessions chosen in this study are in fact relatively short in comparison to whale shark life span, and any bias associated with this violation of instantaneous sampling should be mediated by the compromise of large sample sizes.

3.3.3 Model selection

Burnham and Anderson (2002) argue that traditional hypothesis-testing should be abandoned, and instead a suite of models, each setting out an alternative ecological process, should be compared to see which provides the best explanation of the data. In the context of mark-recapture experiments, this involves building a range of models which promote or constrain various ecological or demographic possibilities, and seeing which one has the most support from the data. Program MARK embodies this approach, with the selection of the best-fit model made using the Akaike Information Criterion (AIC_c) (Akaike, 1973). Essentially, the model with the lowest AIC_c score receives the most support from the data.

Model selection for CJS models can be adjusted for over-dispersion in the data (i.e. where there is more variation in the data than would be expected by random error). The amount of over- or under-dispersion is quantified by calculating median- \hat{c} , also known as the 'variance inflation factor', with deviation > 0 indicating increased over-dispersion of the data.

3.4 Estimating population size and growth rate

Estimates of population size and population growth rate were made using formulations of the Jolly-Seber model (Schwarz & Arnason, 1996) (Figure 3.1). The underlying theory of the Jolly-Seber model is virtually the same as for the CJS

model, but with a crucial difference in the assumptions. Whereas the CJS model conditions on a marked animal following its initial release, the Jolly-Seber model does not, and assumes that both marked and unmarked animals have the same probability of capture. Therefore, any unmarked animals caught during a capture session are assumed to represent a random sample of all unmarked animals present in the population, thus allowing the estimation of population size.

The POPAN formulation was used to estimate population size, returning estimates of apparent survival (ϕ_i), capture probability (p_i), probability of entry (b_i) and superpopulation size (N). In this context superpopulation is defined as the total number of sharks present in the population over the course of the entire study period. Once estimates for parameters ϕ , p , b and N have been estimated through a process of maximum likelihood estimation, population estimates for successive capture sessions can be calculated in an iterative fashion.

The number of new entrants to the population during capture session i can be found as $B_i = Nb_i$. The population size in the first capture session is equal to the number of animals in the population immediately before the start of the study (B_0), which is also estimated during the process of maximum likelihood estimation, although the parameter b_0 cannot be directly manipulated in the program MARK. In subsequent capture sessions, N_i equals the number of sharks remaining in the population from the preceding capture session ($N_{i-1}\phi_i$), plus the number of new entrants (B_i) e.g.;

$$N_1 = B_0$$

$$N_i = N_{i-1}\phi_i + B_i$$

Population trend was investigated using the Pradel- λ formulation (Pradel, 1996). This approach, in addition to returning values for ϕ_i and p_i , also produces a single estimate, or a series of estimates, for population growth rate (λ), having included this parameter in the likelihood function.

4.0 RESULTS

4.1 Data collection

Reported whale shark encounters were not distributed evenly throughout quarterly capture sessions, with a general increase in data submissions in the final two years of the study period. Furthermore, intensive research activity during months May to June 2006-2008, and November-December 2008, heavily supplemented the number of data submissions received during these periods (Figure 4.1). There was a distinct contrast in both the quantity and quality of researcher-collected data, which presented problems during later mark-recapture analysis (see *Discussion*).

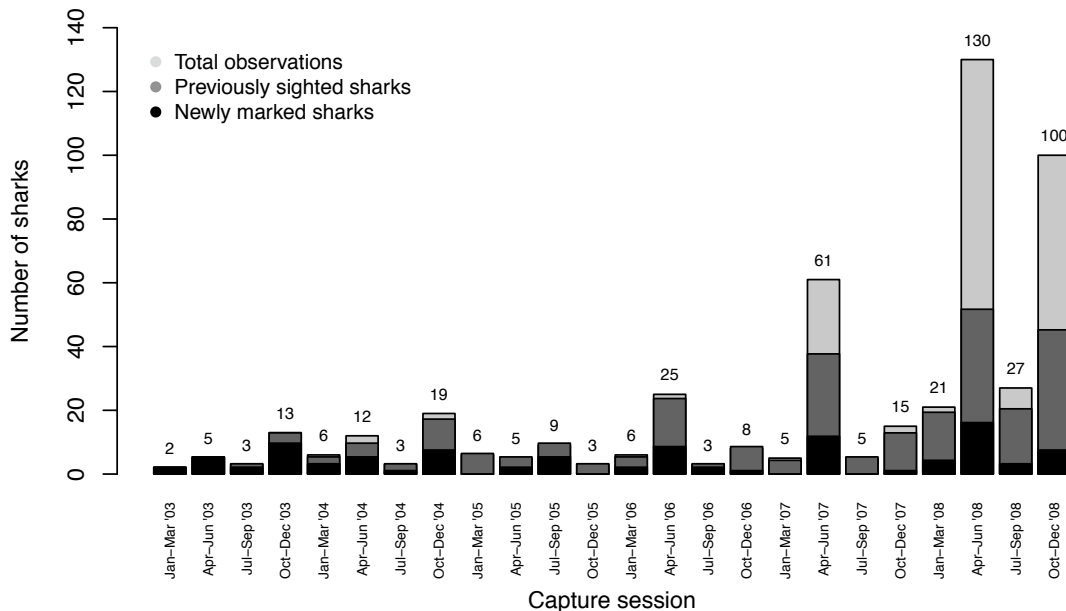


Figure 4.1 Overlaid bars showing absolute numbers of previously unmarked sharks (black shading), marked sharks captured in earlier sessions (dark grey shading) and total identifications made (light grey shading). The extent of light grey shading indicates the number of sharks re-captured *within* a capture session. Text values indicates the total number of data submissions per session.

Within capture sessions the number of unique sharks identified was directly related to the number of reported encounters, although there is some suggestion

that an asymptote is reached at around 40-50 identified individuals (Figure 4.2b). Despite an increase in effective sample size (number of data submissions) during later capture sessions, the absolute number of unmarked (new) sharks encountered remained relatively constant, although the proportion decreased throughout successive capture sessions until stabilising at around 0.2 (Figure 4.2a).

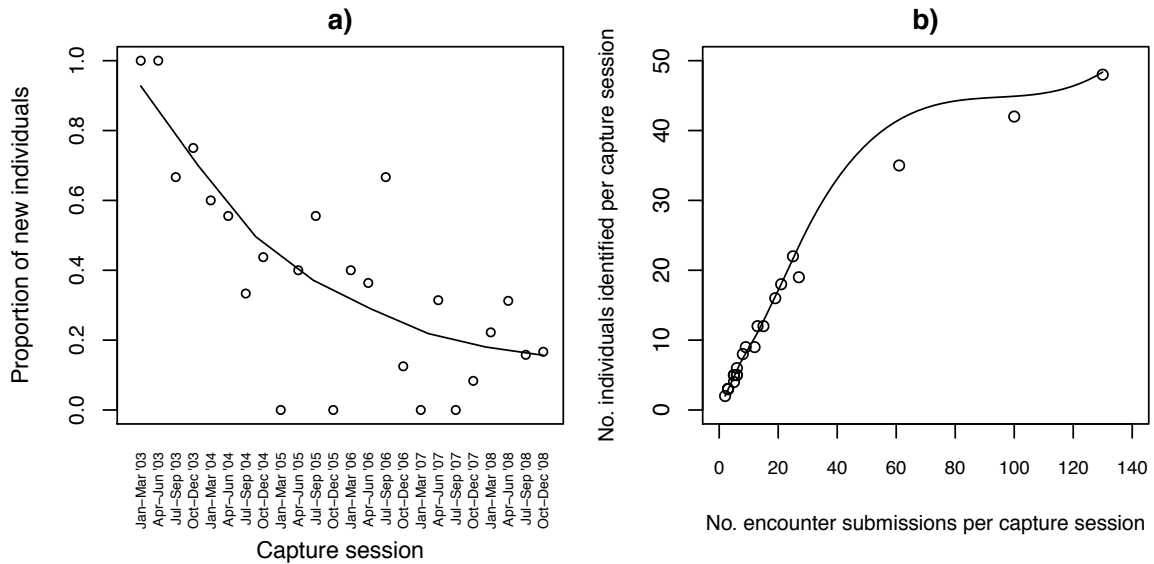


Figure 4.2 a) The proportion of previously unmarked (new) sharks identified during successive capture sessions; **b)** the curvilinear relationship between sample size and number of identified individuals. Lines in both plots are fitted using loess.

4.2 Population structure

From a total of 604 photographic encounter submissions, positive identifications were made from 580 (96%) encounters. The proportion of encounters from which positive identifications could be made increased over the study (Figure 4.3). Non-identification was typically the result of poor photograph quality and poor light conditions. Duplicate encounters from the same day were removed, leaving 562 encounters available for analysis.

In total, 106 individual sharks were identified between 2003-2008. Of these individuals, 77 (73%) were male; 4 (3%) were female; and the remaining 25 (24%)

could not be sexed. Estimated measurements of total length were distributed normally between 3 m - 9 m TL, with a single peak around the mean of 6.07 m TL.

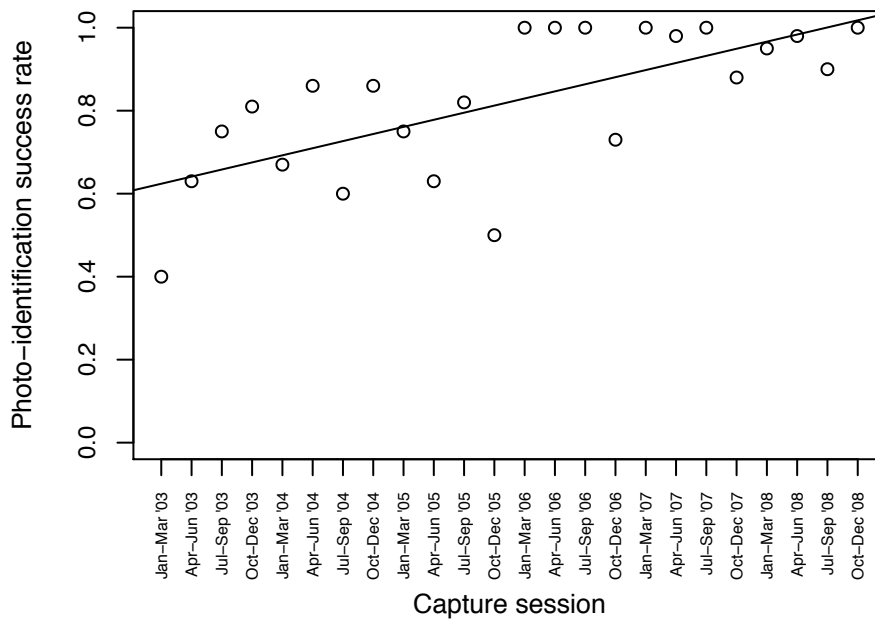


Figure 4.3 Regression between the proportion of encounters leading to positive identifications (photo-identification success) and time.

4.3 Geographic and temporal distribution

Whale sharks were recorded in 4 distinct atolls (Appendix 1), although the vast majority of sightings came from two areas; Baa Atoll (12%) and South Ari Atoll (87%). Encounters were not evenly distributed throughout atoll regions, with prominent areas being Maamigili in South Ari Atoll with 303 of 489 (63%) regional sightings, and Hanifaru in Baa Atoll with 62 of 65 (93%) regional sightings.

Owing to this clustering of data, investigation of temporal distribution was limited to South Ari Atoll and Baa Atoll only. For South Ari Atoll, opportunistic data were available throughout the year, whereas researcher-collected data was restricted to May-July, and were therefore omitted for this analysis. Aggregation of sightings by month shows that whale sharks are encountered year-round in South Ari Atoll, with some suggestion of seasonal peaks during April-May and October-November. Encounter data for Baa Atoll were only available for 2007 and 2008,

although there is a clear seasonal peak in sightings during the south-west monsoon season (May–November) (Figure 4.4).

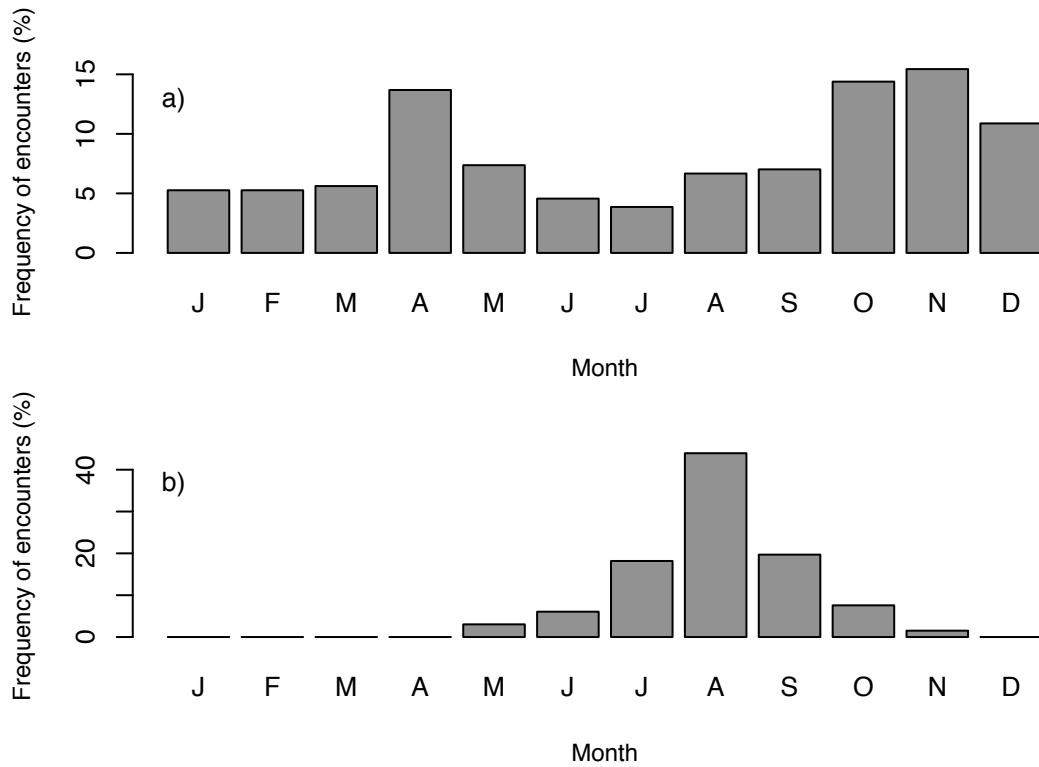


Figure 4.4 Temporal distribution of reported whale shark encounters for a) South Ari Atoll, and b) Baa Atoll.

4.4 Re-sighting rate and residency intervals

Figure 4.5a shows the distribution of re-sighting frequency for individual sharks, with 69 of 106 (65%) sharks being encountered in more than one capture session (i.e. resident) during the six-year study period. The remaining 37 (35%) sharks, recorded during only a single capture session are defined as transient. However, 12 of these individuals were encountered only in the final capture session and were given no chance for further re-sighting.

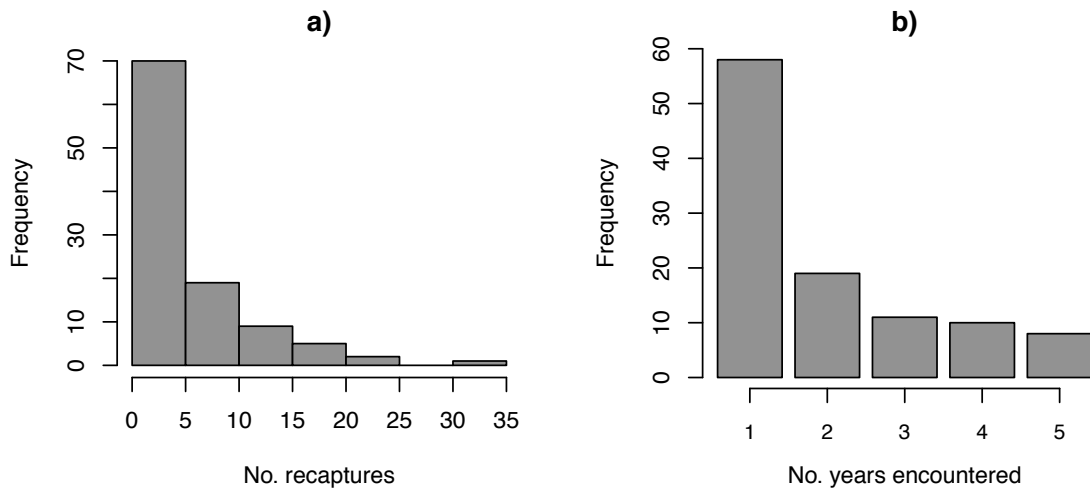


Figure 4.5 a) Re-sighting frequency distribution; b) total number of years in which individual sharks were encountered in South Ari Atoll.

The interval between first and last re-sighting suggests that the majority of sharks sampled in the region throughout the study remained within the population following their initial capture (Figure 4.7). The number of days between successive re-sightings ranged between 1 and 1,300 days, with 75% of re-sightings occurring within 185 days (6.1 months) of the last (Figure 4.6a). The maximum time interval between the first and last sighting was 2,105 days (5.76 years), although due to the high number of new sharks marked late in the study, the average residency interval was less than 1 year (Figure 4.6b).

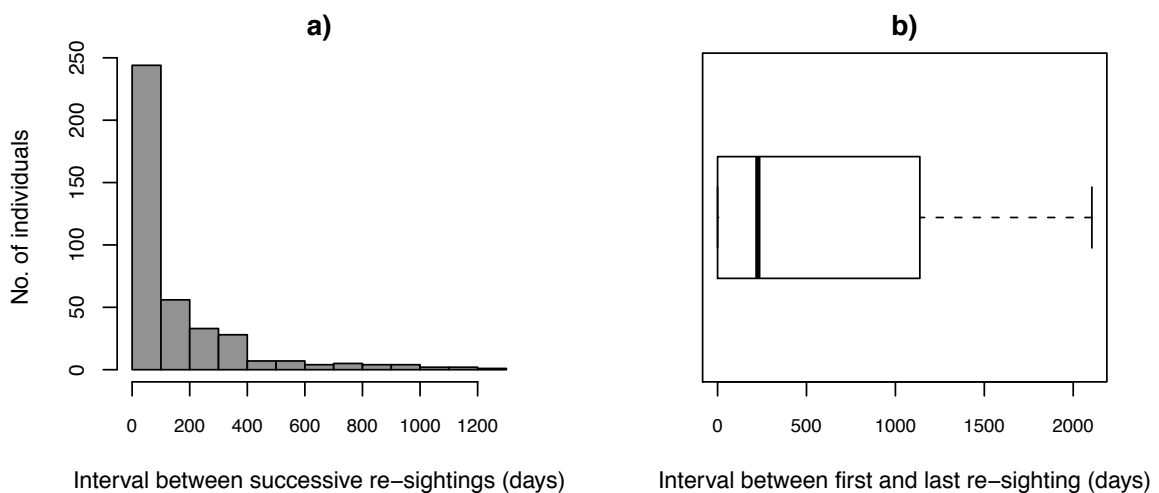


Figure 4.6 a) Distribution of time intervals (days) between successive re-sightings; b) time interval (days) between the first and last sighting for sharks seen two or more times.

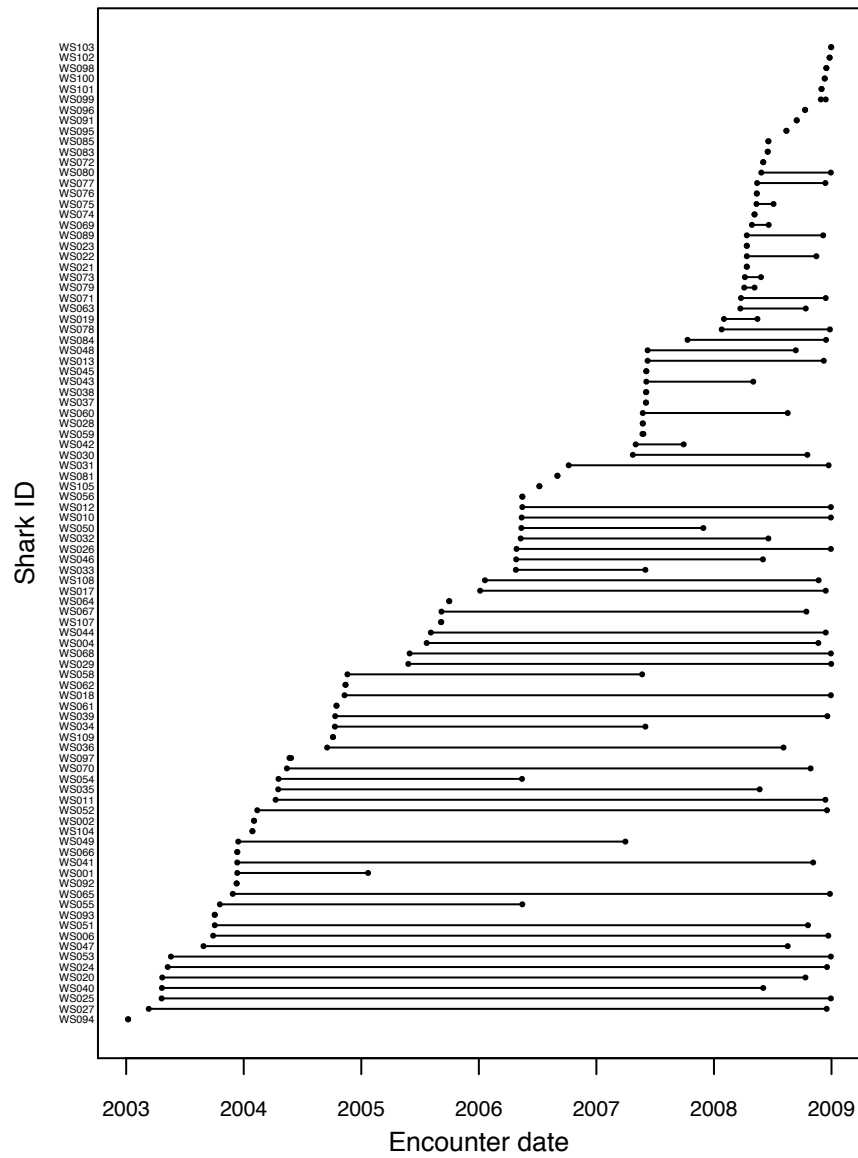


Figure 4.7 Residency intervals for individuals within the South Ari Atoll population, with the date of first and last sighting plotted. Single points indicate that an individual was not re-sighted after the initial encounter, and line length indicates residency interval.

4.5 Mark-recapture analysis

4.5.1 Rejection of population closure

The time scale of the observations leads us to expect an open population, and statistical methods by Otis et al (1978) and Stanley & Burnham (1999) were used to confirm this in South Ari Atoll population - the only area where data were sufficient for mark-recapture analysis. Although the chi-squared test by Stanley & Burnham indicated a p-value greater than 0.05, the value of $p = 0.072$ approached conventional significance, indicating tentative rejection of a null hypothesis of population closure. The test by Otis et al corroborated this with another low p-value ($p = 0.004$).

4.5.2 Goodness of fit

The data showed a good general fit to the underlying model assumptions ($p = 0.55$), and CJS model ranking needed no adjustments as the data showed only minor under-dispersion (median- $\hat{c} = 0.97$). The statistic for trap dependence generated by Test2.CL gave a no compelling indication of trap-dependence ($z = -1.14$; $p = 0.26$). A more detailed look at Test3.SR, which is used to determine if the probability of remaining in the population until capture session i_{+1} is a dependent on being captured in capture session i , gave a strong indication of transience in the population ($z = 3.55$; $p < 0.001$).

4.6 Apparent survival rate

With confirmation of open population dynamics, a Cormack-Jolly-Seber model was used to investigate apparent survival (ϕ_i) between capture sessions, and capture probability (p_i) within capture sessions. Initially a best-fit model of $\phi[.]p[time]$ estimated a high and constant apparent survival rate per quarter ($\phi = 0.96 \pm 0.10$), indicating that marked sharks initially maintained a high probability of remaining within the South Ari Atoll population. In contrast, estimates of p_i

varied quite dramatically between capture sessions under this initial model (Figure 4.6a).

Variation in p_i over time implies that the chance of capturing a marked individual varies between capture sessions. The variation in p_i from South Ari Atoll showed no obvious seasonal pattern, which might have suggested concerted movement of resident groups of sharks, but instead appeared to be strongly related to the overall number of captures within a capture session. This makes intuitive sense, as the greater the number of sharks captured, the more likely it is that a marked individual will be included in the sample.

In an attempt to improve on the estimates of capture probability, sample size per capture session, which in this context is a measure of capture effort, was incorporated into the model as a linear constraint. Despite this, p_i continued to spike during several capture occasions (Figure 4.8b), namely those which overlapped with research activity. Furthermore, the effort-constrained model $\phi[.]p[effort]$ had less information-theoretic support than the less parameterised configuration, and thus the original non-constrained model remained the best-fit.

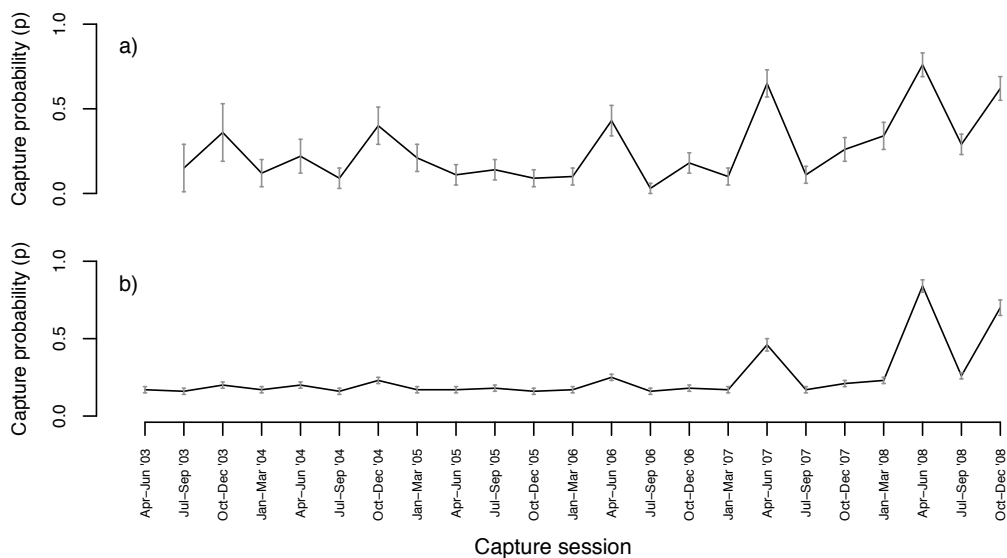


Figure 4.8 Time-dependent CJS estimates of capture probability without (a) and with (b) effort included as a linear constraint.

4.6.1 Time-since-marking approach

Transient animals potentially introduce a negative bias on apparent survival estimates when pooled with residents in CJS analysis, violating the assumption that all marked individuals have the same probability of capture (Williams et al, 2001). As evidence of transience was found during goodness of fit testing, a time-since-marking (TSM) model was employed in an attempt to improve on estimate precision.

A TSM model was designed to produce two estimates of apparent survival; one estimate for the initial interval following marking (thus representing both transient and resident animals), and one constant estimate for all successive intervals (representing resident animals only). With a best-fit model $\phi[M2+]p[time]$, apparent survival rate was estimated at 0.72 ± 0.06 per quarter for sharks in the initial post-capture interval, and 0.98 ± 0.01 per quarter for sharks during all subsequent intervals. The dominant weighting of the TSM model (Table 4.1) is expected given the evidence for transience found during goodness of fit testing, and the resulting estimate of ‘resident’ apparent survival rate (i.e. 0.98 ± 0.01 per quarter) is improved somewhat from the one originally produced by the model $\phi[.]p[time]$.

Model (CJS)	AIC _c	AIC _c Weight	Parameters
$\phi[M2+]p[time]$	849.42	0.99945	25
$\phi[.]p[time]$	864.42	0.00055	24

Table 4.1 CJS time-since-marking model AIC_c ranking and weight, as produced in program MARK.

This high apparent survival rate suggests that sharks which do not immediately leave the population have a high initial probability remaining for extended an period, although this probability does decay over time. The probability of a resident shark remaining in the population for 12 months would therefore be

approximately 0.92 (0.98⁽⁴⁾) and the probability of a resident shark remaining in the population throughout the entire study period is approximately 0.62 (0.98^(4*6)).

4.6.2 The effect of size on apparent survival

To extend survival analysis and aid in the interpretation of apparent survival estimates, a CJS model was constructed to investigate if ϕ_i differed between sharks in two size classes; small (< 6.01 m TL; n = 58), and large (> 6.01 m TL; n = 37). The best-fit model $\phi[M2+]p[time]$ merged both size groups to produce a single parameter estimate, improving only slightly on the next best model $\phi[M2+*size]p[time]$ (Table 4.2). This latter model estimated a lower apparent survival rate per quarter for larger sharks in the interval directly following marking, suggesting smaller sharks are more likely to remain within the resident population following their initial capture (small, $\phi = 0.76 \pm 0.07$; large, $\phi = 0.67 \pm 0.10$), and that they also have a marginally higher apparent survival rate (small, $\phi = 0.98 \pm 0.01$; large, $\phi = 0.97 \pm 0.2$). The selection of the more parsimonious model suggests that although there is evidence from the data that apparent survival does differ between the two size classes, the divergence is relatively small and does not dramatically improve the fit of the model to the data.

Model (CJS)	AIC _c	AIC _c Weight	Parameters
$\phi[M2+]p[time]$	849.42	0.868	25
$\phi[M2+*size]p[time]$	853.18	0.132	24

Table 4.2 CJS time-since-marking model AIC_c ranking and weight, as produced in program MARK.

4.7 Abundance estimation

Advancing from basic survival analysis, a POPAN model was constructed to estimate the size of the South Ari Atoll population. Abundance estimates are extremely sensitive to heterogeneity in capture rate between individuals, and as such are prone to bias (Williams et al, 2001). To limit heterogeneity in capture rates

over time researcher data were omitted (see *Discussion*), and further abundance estimates were made only from opportunistic data.

The model $\phi[.]p[time]b[time]N[.]$, with an AIC_c weight of 100%, estimated a superpopulation of 83-107 individuals. Successive abundance estimates under the POPAN formulation showed a small but gradual increase over the course of the study (Figure 4.8), although this does not necessarily reflect a true increase in abundance due to the potential violation of Jolly-Seber model assumptions.

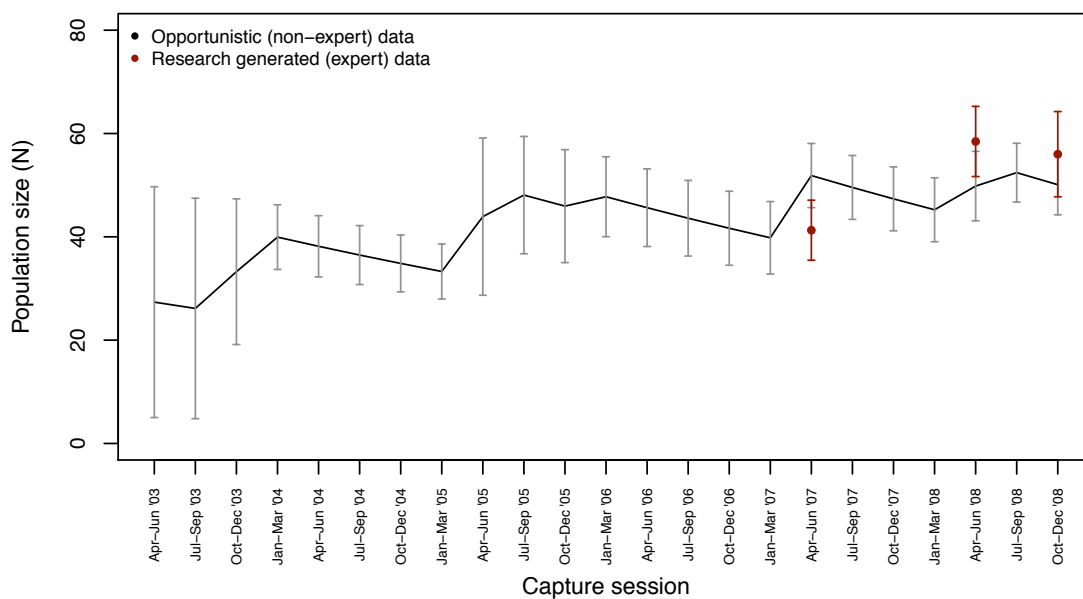


Figure 4.9 Jolly-Seber POPAN abundance estimates for each capture sessions with two data sets; non-expert collected data (black line) and expert collected data (red points).

Research-collected data differed considerably in quality and quantity to opportunistically collected data, and consequently were less likely to result in estimator bias (see *Discussion*). As such research data were extracted and used to produce an independent POPAN model for the period 2007-2008. The best-fit model $\phi[.]p[.]b[time]N[.]$ only had an AIC_c weight of 57%, and so estimates of five models (Table 4.3) were averaged.

The model-averaged superpopulation size was estimated to be between 82-99 individuals for the two year period, a similar range to that estimated for the entire six-year study period using opportunistic data. Point abundance estimates produced using expert data were not markedly different to those generated using non-expert data (Figure 4.9), which goes against the expectation of greater estimate bias resulting from the using opportunistic, non-expert data.

Model (POPAN)	AIC _c	AIC _c Weight	Parameters
$\phi[.]p[.]b[time]N[.]$	193.96	0.571	6
$\phi[.]p[time]b[time]N[.]$	196.91	0.187	8
$\phi[time]p[time]b[time]N[.]$	197.49	0.097	9
$\phi[time]p[effort]b[time]N[.]$	198.02	0.075	9
$\phi[effort]p[time]b[time]N[.]$	198.18	0.069	9

Table 4.3 Jolly-Seber POPAN model AIC_c ranking and weight, as produced in program MARK using expert-collected data only.

4.8 Population growth rate

With POPAN estimates giving no suggestion of a decline in the population, and in fact perhaps even suggesting some population growth, the population growth rate was estimated to assess the magnitude of this change. The Pradel- λ formulation estimates population growth rate (λ) as the ratio of successive population sizes between capture sessions, although absolute estimates of abundance are not made. Using the *sin* link function within MARK, models did not reach numerical convergence unless λ was held constant. The resulting best-fit model of $\phi[.]p[time]\lambda[.]$, with an AIC_c weight of 100%, estimated that the population was growing by approximately 2% per quarter ($\lambda = 1.02 \pm 0.01$). This rate of growth is similar to the trend seen in successive abundance estimates made using the POPAN model, which is expected given that the two Jolly-Seber models are closely related.

5.0 DISCUSSION

5.1 Population ecology

Given the heavily biased sex ratio and absence of mature individuals, it appears that the demographic structure of the whale shark population at South Ari Atoll is similar to other studied whale shark aggregations (Stevens, 2007; Schmidt et al, 2009). However, in marked contrast to these other populations, the majority of sharks in the South Ari Atoll population display high re-sighting rates and lengthy residency periods.

Whale shark are reported to occur throughout the whole of the Maldives archipelago (Anderson & Ahmed, 1993), although data in this study were only available for a relatively small region. Therefore, it is unclear if the population structure and pattern of residency observed in the central atolls is homogeneous throughout the entire archipelago. However, the movement of individuals within the archipelago provides some indication that regional populations are not discreet.

Although this study has found no evidence for long distance migrations to and from the Maldives, individuals do undertake short term migrations within, and possibly just outside (R. Rees, personal communication), the archipelago. Photo-identification has revealed that whale sharks undertake at least one seasonal migration, with 17 individuals recorded from South Ari Atoll being encountered in Baa Atoll during the between May and November feeding season. Such migrations may be more widespread, especially with the occurrence of other seasonal aggregations similar to Baa Atoll reported elsewhere in the Maldives (G. Stevens, personal communication). Given the evidence for movement within the archipelago, the population observed within South Ari Atoll may in fact be representative of the wider Maldivian population.

5.2 Apparent survival estimates

5.2.1 Using opportunistic data with CJS models

In the context of this study, the terms 'capture' and 're-capture' are defined as the successful identification of an individual from an encounter record. Submission of data from third-parties (i.e. tourists) is voluntary, and consequently the volume of reported encounters is not likely to be well correlated with the true number of sharks observed in the study area. It is instead a product of

- i) the number of whale sharks encountered by potential contributors (which not only depends on the abundance of sharks in the population, but also on the amount of tourism or research activity in the area)
- ii) the number of encounters containing images which are submitted (which depends on the availability of underwater cameras, knowledge of the research project and willingness-to-participate)
- iii) the success rate of photo-identification (which depends mainly on image quality).

Of the three factors influencing the number of captures, encounter frequency is most likely to remain relatively constant due to the low demographic turnover of whale sharks and the stability of the tourism industry. However, the other two factors are anticipated to have a more random influence over time.

The probability that an encounter is reported along with a photograph depends entirely on the individual who swam with the shark, and considering the high turnover of tourists visiting the area submission rate is likely to vary dramatically over time. However, it may be argued that whale shark research activity in the South Ari Atoll area during 2007 and 2008, which engaged with local tourist resorts and produced educational materials, increased both knowledge of this study and willingness-to-participate in the scheme. This may at least partially explain the overall increase in submission rate in the last two years of the study.

Photo-identification success rate was generally high throughout all capture sessions, although it did improve over time. In the later sessions, this increase can be attributed to both an improvement in overall image quality associated with modern digital cameras, and an increase in the number of images which clearly show spot-patterns and other key identification areas. The latter may also be result of knowledge-sharing between researchers and resort staff - who in turn instruct tourists - about which areas are useful in the photo-identification process.

Mark-recapture analysis does not require that the entire population is captured during each sampling period, although the greater the proportion captured the more accurate resulting estimates are likely to be. However, if changes in effort influence the proportion of the population which is sampled, this may effect model outputs and should therefore be taken into account.

Sample size per capture session was translated as capture effort and introduced into a CJS model to investigate how this influenced capture probability. The resulting model showed that although this proxy for effort did explain most of the variation in p_i , the probability of recapturing a marked individual remained disproportionately high in the four capture sessions which overlapped with research activity.

During these periods, the relationship between sample size and the number of individuals identified was actually relatively weak. This can be explained by high survey effort effectively sampling all, or almost all, of the individuals present in the population at that time, with further captures simply resulting in re-sightings. In contrast, during capture sessions where survey effort was lower, not all individuals were sampled, and the relationship between sample size and captures remained strong. Therefore, because the constrained CJS model computes capture probability as a function of effort, spikes in capture probability persist in those periods where this relationship falters.

5.2.2 Violation of CJS model assumptions

Despite the variation in capture probability between capture sessions estimates of apparent survival remained unaffected due to high recapture rate and long residency times of sharks within the study population. The high number of intra-session re-sightings during several capture sessions suggests that a significant proportion of the population was sampled, especially in the final three years of the study. By this virtue, the accuracy of apparent survival estimates should be relatively high, although some bias may result if the CJS model assumptions are not fully met.

Heterogeneity in capture probability between marked individuals can result when photo-identification is influenced by photograph quality. Individuals with clear physical markings, such as scars or missing appendages, are more likely to be identified from poor quality images or from photographs where spot patterns are not visible, thus increasing the capture rate of these individuals and ultimately leading to minor negative bias in survival estimates (Williams et al, 2001). However, the number of individuals with clearly identifiable, non-spot-pattern markings was relatively small, and consequently this bias is probably quite limited.

Capture rates may also vary between individuals if there is a geographic shift in the area surveyed over time, which is a possibility when opportunistic data collected from the tourism industry are used (Holmberg et al, 2008, 2009). During this study the extent of surveyed area increased, but none of the original survey areas were neglected in later capture session. As a result, capture rates of sharks marked early in the study were unlikely to have been reduced and model estimates were unlikely to have been biased by this effect.

5.2.3 Interpretation of apparent survival estimates

The high estimates of apparent survival produced by the CJS model, and the lengthy residency periods observed in South Ari Atoll, suggest relatively little loss from within the resident population over at least a period of several years, although population turnover is evident over the full six years of the study. However, it is slightly ambiguous as to whether any loss which does occur is a result of permanent emigration or mortality, although there is some suggestion from the data that the former is a greater driver.

Whale sharks have almost no natural predators when fully grown (Martin, 2007), although they are vulnerable to boat strike, which may result in death (Speed et al, 2008). Although apparently safe from fishing within national waters, recent satellite tagging of whale sharks from the Maldives has shown that individuals temporarily leave the archipelago for periods of several weeks (R. Rees; personal communication), potentially coming into contact with foreign fishing vessels. Despite this, the risk of mortality is probably still relatively low.

Given the demographic and social structure of whale sharks in the Maldives, it can be assumed that at some point individuals do leave the population permanently, possibly upon maturity. If this is indeed a driver of permanent emigration it may be assumed that, given the information on length at maturity, large sharks are more likely to mature and leave the population within the bounds of the six-year study than smaller sharks.

Survival analysis using a size-specific CJS model did estimate a marginally lower apparent survival rate for larger sharks, indicating that sharks from this group have a higher probability of leaving the population. This lends support to the hypothesis that loss to the population is driven primarily by emigration of larger sharks, perhaps when individuals reach maturity.

5.3 Population size estimates

5.3.1 Using opportunistic data with POPAN models

Jolly-Seber models are not conditional on marked individuals, and the enumeration of unmarked animals during capture sessions allows for the estimation of abundance. Although Jolly-Seber models incorporate the CJS approach as a foundation for the estimation of capture probability and apparent survival rate, they make different assumptions of the estimated parameters; namely that they apply to both marked and unmarked individuals (i.e. capture probabilities are estimated from recaptures of marked individuals, but are applied to both marked and unmarked sharks). If in reality capture rates differ between marked and unmarked individuals as a result of study design, estimates of abundance are vulnerable to substantial bias (Williams et al, 2001).

Both the nature of the data used in this study and the photo-identification protocol used lead to potential heterogeneity in capture rate between marked and unmarked individuals. The initial marking of a shark requires the provision of a good quality, left-hand side image showing the lateral spot pattern, from which an I3S fingerprint identity is created. However, during later re-captures this spot pattern is not essential, and identifications can be made from poorer quality photographic submissions, essentially making previously marked sharks much easier to recapture.

Throughout most of the study encounter submissions came from untrained observers, and as a result photographs did not always reveal the left-hand spot pattern needed for initial identification. As long as the individual's spot-pattern had been previously registered in the database, recaptures could still be made from these photos, and so, in real-time at least, the probability of recapturing a marked shark was higher than the probability of photo-tagging an unmarked shark, which always required an image of this spot-pattern.

However, the bias caused by heterogeneity in capture rate is limited somewhat by the retrospective nature of photo-identification. A photograph provides a permanent visual record of an animal, and as such can be referred to again if an identification was not initially forthcoming. If a shark is re-sighted several times, any one of these encounters can potentially yield an image suitable for I3S identification, and earlier images can then be matched to the individual accordingly. However, if a suitable image is consistently missed, then heterogeneity remains.

An additional complication comes from variation in the strength of this heterogeneity over time. For example, if unmarked sharks are consistently less likely to be captured throughout the study, abundance will be constantly underestimated. If however unmarked sharks become easier to catch, for whatever reason, negative bias will become less and estimates of population size will increase.

Expert encounters followed a defined protocol that ensured photographs of each shark were suitable for I3S-assisted identification and consequently the likelihood of capturing marked and unmarked sharks was closer to equal during capture sessions where data were mainly collected from experts. Therefore, in an attempt to limit the effect of time-specific heterogeneity in capture rate, expert submissions were removed from the data.

However, the level of heterogeneity in capture rate probably did still vary over time, with unmarked sharks at the beginning of the study having a lower likelihood of capture if they were not seen again, or if future photos still did not allow for I3S identification. In this situation the model estimates for early capture periods would be negatively biased. The gradual increase in abundance observed in the POPAN estimates may therefore be a product of greater equality in the capture rates of marked and unmarked sharks, and not necessarily indicate a true increase in population size.

5.3.2 Using expert data with POPAN models

Given that the data provided by researchers was greater in both quantity and quality, it would be expected that POPAN models run exclusively with this data are more robust to bias, and as such would produce more accurate estimates. However, the resulting abundance estimates were very close to those made by the models using non-expert data, suggesting that opportunistic data collected later in the study allowed for equally good mark-recapture analysis. This can presumably be explained by an increase in submission rate of non-expert data and improvement in its quality during later capture sessions resulting in both a larger proportion of the population being sampled, and heterogeneity in capture rate being reduced.

Further support for the POPAN model estimates comes from the raw data. Within three research periods, where survey effort was relatively intense, the high number of re-sightings suggests that all, or almost all, of the sharks present within the population were sampled. In these sessions the number of individuals identified fell within the bounds of the population estimates generated by the POPAN model.

5.3.3 Interpretation of POPAN abundance estimates

The POPAN model produces two types of abundance estimate; successive population sizes for each capture session, and a single superpopulation size which represents all individuals ever present in the population over the course of the study. The size of the superpopulation at South Ari Atoll was estimated at around 90 individuals, although quarterly abundance estimates remained relatively constant at approximately 40 individuals, implying some degree of population turnover in the six years between 2003 and 2008.

With both losses and gains occurring within a population, turnover is to be expected. However, the extent of turnover as suggested by POPAN model

estimates is surprisingly high considering that the principle driver of loss appears to be emigration of maturing individuals. However, given the observation of transiency in the population, with approximately one third of all individuals encountered only once, the short term presence of these vagrant individuals would push up size of the superpopulation more than would otherwise be expected by population turnover alone.

5.4 Population growth rate

Under the Pradel- λ approach, population growth rate is estimated as the ratio of abundance estimates in successive capture sessions. This process does not involve the absolute estimation of abundance, and therefore heterogeneity in capture rate between marked and unmarked individuals is less problematic as long as any heterogeneity remains constant throughout the study.

As previously discussed, the upward trend observed in POPAN abundance estimates is likely a result of a difference in capture rate between the beginning and end of the study, with earlier estimates being negatively biased, and this same heterogeneity is likely to influence Pradel- λ model estimates of population growth rate in a similar fashion. Therefore, the estimated population growth is likely to be subject to positive bias, and should be treated with caution.

6.0 RECOMMENDATIONS & FURTHER WORK

This study has demonstrated that opportunistic data collected from non-experts in the Maldives can be used to investigate whale shark life history traits using mark-recapture methods, although a series of recommendations can be made to improve further monitoring and research work:

- ▶ Within South Ari Atoll there is no compelling evidence for a decline in the population, and as such intensive monitoring activity is perhaps unnecessary. Therefore, given that there was little difference between model estimates using expert and non-expert data, it is recommended that collection of opportunistic data continues.
- ▶ Furthermore, with whale shark research activity becoming more established in the South Ari Atoll area, there is great opportunity to improve the quality of this opportunistic data through education of tour operators and tourists. Whale shark encounter *Code of Conduct* and photographic submission guidelines should be distributed amongst tour operators, with the joint aim to promote responsible ecotourism and to promote the conservation aims and research goals of the Maldives Whale Shark Research Programme.
- ▶ Particular emphasis should be on the collection of opportunistic data from novel areas, potentially involving collaboration with safari boat operators. These data will help to i) define the range of whale sharks within the Maldives; ii) glean information about movement both within the archipelago and into foreign waters; and iii) to improve knowledge of whale shark residency time within the Maldives.

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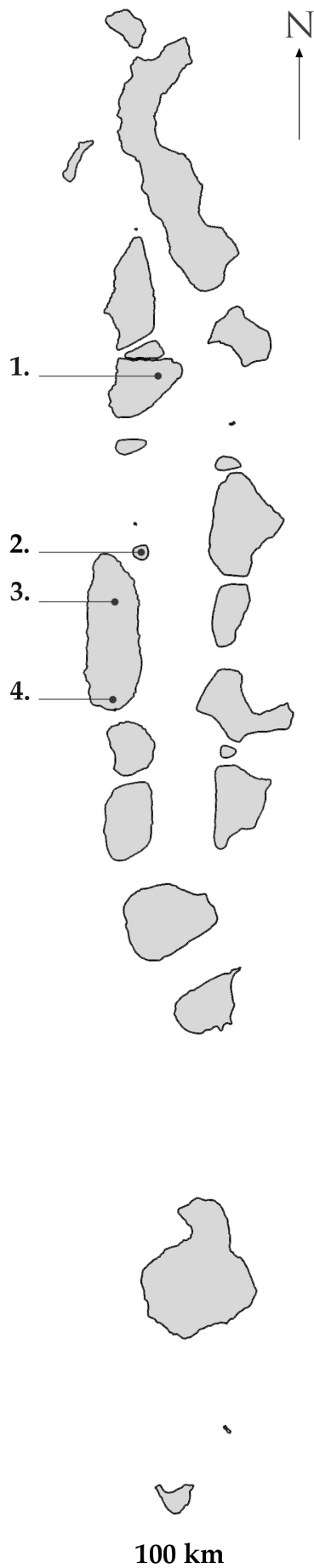
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A1. APPENDIX 1



Appendix 1. Location and number of encounters for each atoll and reef within the Maldives. Text numbers on the map correspond to the four atolls from which encounters were recorded. Map modified from Anderson & Waheed (1999).

Location	Encounters
1. BAA ATOLL	65
Dhigu Thila	2
Hanifaru	61
Landaa Giraavaru	1
Nelivaru Thila	1
2. RASDHOO ATOLL	3
Rasdhoo Madivaru	3
3. NORTH ARI ATOLL	4
Kudadhoo	4
4. SOUTH ARI ATOLL	489
Bodu Finolhu	2
Dhangethi	2
Dhigurah	18
Dhihoo	7
Fenfushi	2
Ghuraidhoo	1
Kudurah	1
Maamigili	303
Nalaguraididhoo	1
Rangali	5
Vilamendhoo	8
White Sands	34
Unspecified	102
UNKNOWN ATOLL	2