

Seeing Spots: Photo-identification as a Regional Tool for Whale Shark Identification

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Abstract—The identification of individual animals over temporal and spatial scales can provide robust estimates of population size and distribution. While marker tagging can provide an option to achieve this, it can be problematic both in terms of tag loss and the associated difficulties and effects of attaching the tags. Photo-identification of distinctive characteristics which remain stable over time has replaced tagging in some species but usage at regional scales has been hampered by a lack of standardisation of matching methods. We describe the use of a semi-automated computer program (I³S) for matching the spot patterns of whale sharks, *Rhincodon typus*, in the Seychelles aggregation and compare this to images captured from other areas in the Western Indian Ocean. Sharks totalling 443 individuals were uniquely identified in the Seychelles from 2001 – 2009, 109 of which were seen in multiple years. Conventional open mark-recapture models for 2004 – 2009 gave an abundance estimate of 469 to 557 sharks (95% C.I.). I³S digital fingerprints were shared with researchers in Djibouti, Mozambique, and Tanzania and, while no matches were found between locations, the ease with which regional comparisons were made will help to define whether the shark populations in these areas are distinct, enabling long-term and broad-scale regional comparisons.

INTRODUCTION

Whale sharks (*Rhincodon typus*) are pan-oceanic planktivores that were first described from a specimen captured in the Western Indian Ocean in 1828 (Smith, 1828). They are listed by the IUCN as Vulnerable (VU A1bd+2d) based on observed reductions in landings, actual levels of exploitation and because further population decline is deemed likely to occur if

directed fisheries remain unmanaged (IUCN, 2009). In November 1999, the whale shark was added to Appendix II of the Convention on Migratory Species (CMS) as “a species whose conservation status would benefit from the implementation of international co-operative Agreements”. The species was also listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) in November 2002.

Despite broad international interest in the conservation status of whale sharks, relatively little is known about regional population sizes or trends in abundance. Some local declines in the Indian Ocean have been linked to targeted fisheries (Anderson & Ahmed, 1993; Hanfee 2001; Theberge & Dearden, 2006). In Western Australia, a decline in shark abundance and average body length based on tourism operator-collected data was attributed to fishing in other areas of this population's range (Bradshaw *et al.*, 2007 & 2008); however, this decline has been debated (Holmberg *et al.*, 2008, 2009). The need to quantify the population abundance of whale sharks at both local and regional (oceanic) scales thus remains a priority for conservation management.

In the Western Indian Ocean, whale sharks are known to aggregate seasonally around the islands of the Seychelles (Rowat, 1997; Fowler, 2000; Rowat & Gore, 2007). The temporal and spatial extent of their distribution has been monitored intensively since 2001 and it has been found that the population comprises a mixture of both site-faithful and migratory individuals (Rowat *et al.*, 2008; Rowat *et al.*, 2009a). Seasonal aggregations are also known to occur in various other coastal sites throughout the Indian Ocean, specifically Djibouti (Rowat *et al.*, 2006), Madagascar (Jonahson & Harding, 2007), the Maldives (Anderson & Ahmed, 1993), Mozambique (Speed *et al.*, 2008), South Africa (Cliff *et al.*, 2007), Tanzania (Mahingika & Potenski, 2009) and Western Australia (Meekan *et al.*, 2006).

Whale sharks need to be uniquely identified to monitor demographics and estimate population numbers through Catch-Mark-Recapture (CMR) modelling techniques. Sharks can be uniquely identified by spot patterns on their skin, the area posterior to the fifth gill slit being particularly suited to this purpose (Arzoumanian *et al.*, 2005; Speed *et al.*, 2007). With the advent of digital photography, underwater photography has become cheaper and easier; digital image files are also readily manipulated which has promoted the development and use of photo-identification software. Once

individuals are uniquely identified, their re-sighting in subsequent years can be used to develop population abundance estimates. On a regional scale, comparisons can be made between different sites to see if individuals frequent multiple aggregation sites, thereby providing an indirect examination of regional-scale migrations and potentially enabling large-scale population estimates.

METHODS

Study area

Seychelles

The study area has been previously described (Rowat *et al.*, 2009a, b). Briefly, the granitic islands of Seychelles are situated on a shallow continental plateau at 4° S and 55° E in the path of the westward flowing Southern Equatorial Current in the Western Indian Ocean (New *et al.*, 2005). From June to October, seasonal winds blow from the southeast, resulting in localised primary productivity and the appearance of whale sharks and other planktivores such as manta and devil rays (*Manta birostris* and *Mobula* spp.). The study area was the coastal zone around the island of Mahe extending to a maximum of 4 km offshore.

Regional Data

Whale shark photo-ID data were exchanged with other research programmes operating in Djibouti, Mozambique and Tanzania to facilitate regional comparisons.

Identification Studies - Seychelles

Aerial surveys were undertaken from a delta-wing micro-light aircraft (Aquila II, Solo Wings, South Africa) by experienced pilots trained in aerial survey techniques. Survey teams were directed to individual sharks by radio communication with the spotter aboard the aircraft. During the peak season, aerial and boat surveys were carried out on a daily basis, conditions permitting (Rowat *et al.*, 2009b).

Wherever possible, sharks encountered were sexed by the presence (in males) or absence (in females) of pelvic claspers, sizes were estimated by an experienced observer, and any prominent scars or features were noted and photographed for identification purposes. From 2001 – 2004, sharks were opportunistically tagged with marker tags (Rowat *et al.*, 2009a). The focal area for photo-identification was the area posterior to the gill slits where the spot patterns of the sharks have been found to be unique to each individual (Arzoumanian *et al.*, 2005; Meekan *et al.*, 2006; Speed *et al.*, 2007). The patterns on the left and right of each shark, however, are different (Speed *et al.*, 2007) and therefore both sides were photographed to prevent duplicate entries in the database. From 2001 to 2004, photographs were taken opportunistically for potential photo-identification; from 2004, affordable digital underwater cameras increased the number of images collected.

Digital images were matched using the computer program I³S (van Tienhoven *et al.*, 2007), which is an effective tool for semi-automated photo-identification of whale sharks (Speed *et al.*, 2007). I³S allows the user to 'fingerprint' the spot patterns on the skin of a whale shark and compare these to similarly fingerprinted images in the database to see if the shark has been previously photographed.

The images of the area behind the gill slit were opened with the I³S program and three reference points were plotted at (1) the top of the fifth gill slit, (2) the posterior-most point where the pectoral reaches on the body and (3) the bottom of the fifth gill slit. Specifying these reference points allowed the program to re-scale or rotate images as required to ensure standardised comparisons regardless of photographer orientation or distance from the shark. The spots on the shark's flanks were then marked, allowing the program to calculate the position of each marked spot relative to the reference points and to compare the marked spot's position, through linear transformation, with its potential 'pair' on each image in the database (van Tienhoven

et al., 2007). A 'score' was derived from the sum of the distances between the paired spots divided by the number of pairs. The program presented to the user a list of the top fifty highest-ranked matches and the user visually analysed these matches, considering differences in spot selection, other patterning and scarring, to confirm the final selection.

A database of sightings for each individual shark was compiled for tagged individuals and those with I³S identities. This was used to create a combined inter-annual history for CMR models to estimate population size. Photo-identities of both the left and right side were not available for all individuals with I³S identities and so left-side identities were used because these were more common than those for the right-side (381 of 330).

Population estimates were made using conventional CMR modelling software. To estimate the population, assuming a closed population with no net immigration or emigration (demographic closure), we used the program CAPTURE (Otis *et al.*, 1978). This provided goodness-of-fit tests for each model and the program selected the most probable model(s) for the dataset.

For estimation of population size using open population models that do not assume demographic closure, we used the Cormack-Jolly-Seber (CJS) model (Schwarz & Arnason, 1966) in the POPAN option in the program MARK (White & Burnham, 1999). The POPAN option in MARK does not offer a bootstrap goodness-of-fit, so a recaptures-only (CJS) analysis was run in MARK, using the same data to allow a bootstrap goodness-of-fit to the model.

Identification Studies - Regional Data

Whale shark photo-ID data obtained from other organisations within the Indian Ocean were examined and re-processed where necessary for comparison using I³S. The fingerprinted images were then compiled with those from the Seychelles into a regional database to see if any of the sharks were observed at multiple sites.

RESULTS

Identification Studies - Seychelles

Population Demographics

A total of 443 individual sharks were identified using photo ID from 2001-2009. Of these, the sex of 337 individuals was established, 278 (82.5%) being male and 59 (17.5%) female. The mean size of individuals identified each year was 5.8 m (± 1.2 SD), with the highest size class frequency being the 5 – 7.5 m range (51%) followed by the <5 m range (38%) (Fig. 1a). However, there were very few sharks recorded below 4 m (N=23) and, while there were several >7.5 m (N=59), there were very few >10 m (N=2). There was some variation in size between years and between sexes (Fig. 1b) but this was not significant.

The annual number of photo IDs collected rose from 2004, as did the percentage of re-sighted sharks (Table 1). Overall, 109 (24.6%) of the 443 individuals have been sighted in multiple years. Two sharks have been seen in five different years, 11 in four years, 22 in three years and 74 in two years. The longest time-span of sightings was nine years: four sharks first seen in 2001 were also seen 2009 as well as in intervening years. The spot patterns did not change during this period.

Population estimation

Previous attempts to estimate abundance with re-sighting data from marker tags produced estimates with a very high error, largely due to tag loss or deterioration (Rowat *et al.*, 2009a). Only 34 photo identities were captured in 2001 - 2003, so population estimates were only made using the photo ID data from 2004 – 2009.

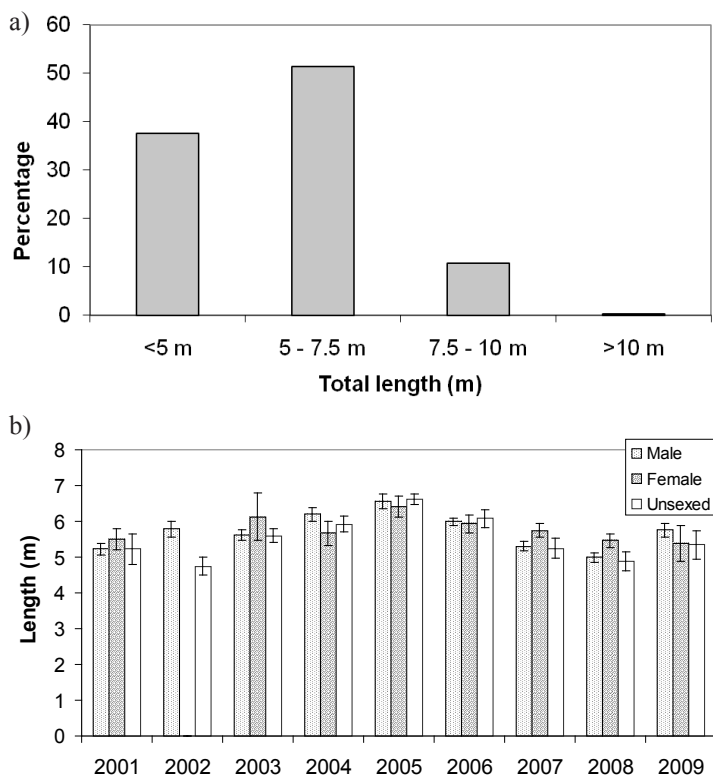


Fig. 1a) Size frequency distribution and b) mean shark length (with standard error) in Seychelles whale shark aggregations in 2001-2009.

Closed population models generated using the program CAPTURE on the latter photo-identification data indicated that a model allowing for variation in the records due to time, behaviour and heterogeneity $\{m(tbh)\}$ was the most appropriate, but no population estimator was available for this model; also, the data violated the assumption of closure ($Z = -5.395$; $P < 0.001$).

In the program MARK, candidate models are ranked by the likelihood of the goodness-of-fit of the data (c) to the individual models based on Akaike's Information Criterion (AIC) values and weights (Akaike, 1973). Bootstrap goodness-of-fit is not available with the POPAN model and we thus first modelled the data with

Table 1. Whale shark photo-identification records for Seychelles for 2001- 2009 with details of new records and re-sightings from previous years.

	2001	2002	2003	2004	2005	2006	2007	2008	2009
Sharks identified (N)	15	0	24	19	114	186	88	68	88
New identifications	15	0	23	19	108	146	49	37	46
Old identifications	0	0	1	0	6	40	39	31	42
% Re-sightings	0%	0%	4%	0%	5%	21%	44%	46%	48%

the recaptures-only model that has this option. The model $\{\Phi(.) p(t)\}$ with time-dependent variability was ranked the highest. However, the bootstrap goodness-of-fit simulation yielded some evidence of over-dispersion ($p = 0.022$), indicating that the probability of capture was not uniform. Using the routine provided within MARK, the calculated over-dispersion was $\hat{c} = 1.253$. Adjusting the AIC accordingly within the POPAN open population models, an abundance estimate of 469 to 557 sharks (95% C.I., S.E. = 22) was ranked the highest. This was based on the constant model $\{\Phi(.) p(.)\beta (.N(.))\}$ (Table 2), with a high probability of capture; however, the level of entry into the population could not be estimated.

Identification Studies - Regional)

Population Demographics

A total of 1069 individual sharks were identified in the western Indian Ocean, Seychelles, Djibouti, Mozambique and Tanzania. This dataset includes individuals identified in 2009

in Djibouti, Mozambique and Seychelles. In all three of these aggregations, the number of males was much greater than females, 76-83% of the individuals being male (Table 3). In the Djibouti aggregation, it was possible to generate a frequency distribution of size classes (Fig. 2) that indicated that 81% ($n=133$) of the individuals identified were between 3 m and 5 m, while a further 15% ($n=25$) were <3 m.

Population distribution

There were no photo-identification matches between the different geographic sites. In Tanzania, 66 whale sharks had been identified by researchers with marker tags over a three year period (Mahingika & Potenski, 2009); however, only three sharks could be used for photo-identification using I³S, none of which matched any of the other sharks in the combined regional data set. None of the sharks tagged in Tanzania were sighted during monitoring activities in the Seychelles.

Table 2. Seychelles whale shark population estimates and parameters derived from Cormack-Jolly-Seber open population model (POPAN option) for the combined photo-identification and tag data for 2004 - 2009, with estimates of apparent survival (Φ), capture probability (p), probability of entry into the population (β) and population size (N)

Real Function Parameters of $\{\Phi(.) p(.)\beta (.N(.))\}$				
Parameter	Estimate	Standard error	95% Confidence interval	
			Lower	Upper
1: Φ	0.382	0.021	0.343	0.423
2: p	0.739	0.024	0.690	0.783
3: β	1.000	<0.001	<0.001	1.000
4: N	506.218	22.11	469.299	556.863

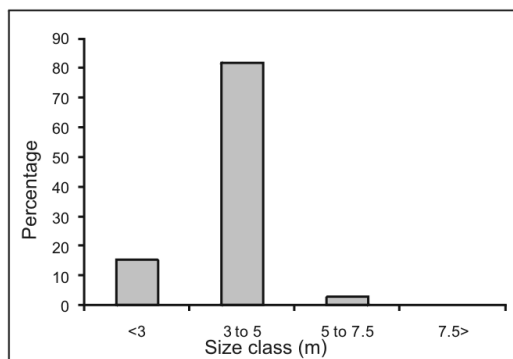
Table 3. Basic population demographics for whale sharks photo-identified in three regional aggregations.

	Sharks (N)	% Male	% Female	Mean size (m)
Seychelles	443	83	17	5.7
Mozambique	366	76	24	6.5
Djibouti	257	83	17	3.7

DISCUSSION

Although monitoring techniques and intensities differed substantially between the locations considered in this study, the results show that the use of standardised photo-identification protocols and software processing enables implementation of inter-site comparisons on a regional scale. While this is the first attempt at a regional comparison, and there may be further regional photo-identities that can be included, to date, photo-matching has yet to show movement of sharks away from the aggregation found in the Seychelles.

All of the aggregations at the sites included in this comparison were dominated by immature male sharks. In excess of 75% of the population were males, with an average size of <8 m in each of the aggregations. Analysis of size frequency classes of Seychelles sharks showed that there has been little variation in the sizes of sharks reported and that there are few small juvenile or adult-sized sharks of >8 m (Fig. 1a). Thus, it appears that, as the sharks reach adult size, they leave this aggregation. In comparison, in the Djibouti aggregation, the average size of sharks was 3.7 m, with 15% of identified individuals being <3 m, only 5% between 5-7.5 m and no larger sharks; as such, this may indicate that there is a further size segregation between neonatal-sized individuals (1-2 m) and those found in the coastal aggregations (4-8 m). The average size and sex ratio of sharks in Seychelles were similar to those reported in Australia (Bradshaw *et al.*, 2007), Belize (Heyman *et al.*, 2001), Mozambique (Simon Pierce pers. comm.) and Maldives (Riley *et al.*, 2010). These sites all have juvenile male-dominated populations. This poses the question as to the location of the adult sharks.

**Fig. 2.** Size frequency distribution of whale sharks in the Djibouti aggregation in 2009.

The problem of poor retention of conventional tags on this species has previously been noted (Graham & Roberts 2007). Photo-identification has provided an estimate of tag retention time and shown the effects this has on the estimation of population abundance (Rowat *et al.*, 2009a). Within the Seychelles aggregation, the addition of a further two years of photo-identification data has confirmed the order of magnitude of the previous population estimate, with lower margins of error: in 2004 – 2007 the estimate was 348–488 (95% C.I., S.E. = 34) compared to 472 – 561 (95% C.I., S.E. = 22) in 2004 – 2009 (Rowat *et al.*, 2009a). This indicates that, in absolute terms, a small population of whale sharks is using Seychelles waters. As with previous estimates, the tests for closure of the population were violated and the rate of entry into the population could not be estimated. These findings are corroborated by the results of satellite tracking studies that have shown that whale sharks move considerable distances away from the Seychelles (Rowat & Gore, 2007). However, the regional comparison made here indicated that there were no matches between the Seychelles, Djibouti, Mozambique

and Tanzania populations, suggesting that the major “known” aggregation sites in the Western Indian Ocean are not sharing whale sharks.

Recent work on the genetic diversity of whale sharks based on haplotype frequency of complete mitochondrial DNA control regions has shown little evidence of geographical clustering (Castro *et al.*, 2007). This is corroborated by microsatellite studies of specimens from the Caribbean, Pacific and Indian Oceans (Schmidt *et al.*, 2009). There was some evidence of separation between Atlantic and Indian Ocean samples, but not between Indian Ocean and Pacific samples (Castro *et al.*, 2007). Although sample sizes in both these studies were relatively small, these findings support those of satellite tracking that show widespread movements of sharks away from the Seychelles (Rowat & Gore, 2007). This would tend to promote interbreeding, at least on ocean-basin scales, leading to low levels of genetic differentiation between regions. However, the high re-sighting rate does indicate at least seasonal philopatric behaviour.

Of note, most of the samples tested in both these genetic studies were taken from known aggregation sites and, where recorded, the sharks ranged from 2.5 - 13.5 m in length, the average being 6.25 m (Schmidt *et al.*, 2009). It has been suggested that the low genetic diversity and lack of structure between geographically separated populations is an indication of high maternal gene flow caused by movement of breeding females (Bradshaw, 2007). This situation may, however, be complicated by a bias in sampling mainly immature individuals at what are almost certainly feeding aggregation sites (Heyman *et al.*, 2001; Nelson & Eckert, 2007; Bradshaw *et al.*, 2007): immature individuals from different breeding populations may aggregate at these feeding sites, thereby masking population separation.

The aforementioned genetic studies both attempted to estimate the effective (i.e. breeding) population size based on generational mutation rates. These estimates ranged from 27,401–179,794 (Schmidt *et al.*,

2009) to 119,000–238,000 females (Castro *et al.*, 2007), although the authors of both studies urged caution in using these values because of the assumptions they made and the small sample sizes. These estimates of the global population appear to be at odds with the population estimate presented here and one for Ningaloo Reef in Western Australia (Meekan *et al.*, 2006), and strongly suggest that transient feeding aggregations do not comprise the only or even the principle communities of this species (Castro *et al.*, 2007).

These findings therefore reinforce the importance of implementing more formal population monitoring in other areas, both within the region and globally. Presently, there are very few locations where adult sharks or pregnant females are found and very little is known of small sharks under 3 m. Until such time that adult (breeding) groups are identified and persistent questions regarding their life-history are answered, in-depth and consistent long-term monitoring of shallow-water aggregations of these sharks is one of the only ways to estimate the status of the species. The results also emphasise the need for an ocean-wide approach to the conservation and management of this, the largest extant shark in the world.

Photo-identification can play a useful role in answering some of these questions. However, due to the fact that whale sharks are slow-growing and are known to frequent particular aggregation sites for long periods, photo-identification cannot be used in isolation as it appears that once they leave these aggregations, the sharks are seldom seen again. These methods need to be used on a long-term basis and in conjunction with other monitoring methods, such as aerial surveys and satellite tagging, to obtain information regarding whale shark migrations and behaviour away from the aggregation sites. Similarly, genetic studies may yet show regional population and even familial relationships if carried out at sufficient intensity. Monitoring needs to be expanded regionally and, in particular, to areas known to have different population demographics.

Data currently being collected in Djibouti may, in years to come, show if the smaller sharks there join other aggregations of larger sharks when they mature or whether there are as yet unknown aggregations in the area. Photo-identities can be captured by personnel with minimal levels of training, which broadens the opportunities for data capture. As long as suitable photos are taken, identities can be established, thus enabling the public to participate in whale shark identification programmes and promote broad-scale regional comparisons.

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REFERENCES

- Akaike H, 1973 Information theory as an extension of the maximum likelihood principle. In: Petrov B, Csaki F (eds) Proceedings of the Second International Symposium on Information Theory, Budapest, Hungary, pp. 267-281.
- Anderson RC, Ahmed H (1993) Shark fisheries of the Maldives, Ministry of Fisheries and Agriculture, Maldives, and FAO, Rome, 81pp
- Arzoumanian Z, Holmberg J, Norman B (2005) An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. Journal of Applied Ecology 42: 999-1011
- Bradshaw CJA (2007) Swimming in the deep end of the gene pool - global population structure of an oceanic giant. Molecular Ecology 16: 5111-5113
- Bradshaw CJA, Mollet HF, Meekan MG (2007) Inferring population trends for the world's largest fish from mark-recapture estimates of survival. Journal of Animal Ecology 76: 480-489
- Bradshaw CJA, Fitzpatrick BM, Steinberg CC, Brook BB, Meekan MG (2008) Decline in whale shark size and abundance at Ningaloo Reef over the past decade: The world's largest fish is getting smaller. Biological Conservation 141: 1894-1905
- Castro ALF, Stewart BS, Wilson SG, Hueter RE, Meekan MG, Motta PJ, Bowen BW, Karl SA (2007) Population genetic structure of Earth's largest fish, the whale shark (*Rhincodon typus*). Molecular Ecology 16: 5183-5192
- Cliff G, Anderson-Reade MD, Aitken AP, Charter GE, Peddemors VM (2007) Aerial census of whale sharks on the northern KwaZulu-Natal coast, South Africa. Fishery Research 84: 41-46

- Fowler S (2000) Whale Shark, *Rhincodon typus*, policy and research scoping study. Nature Conservation Bureau, Newbury, UK. 27pp
- Graham R, Roberts CM (2007) Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. Fishery Research 84: 71-80
- Hanfee F (2001) Trade in whale shark and its products in the coastal state of Gujarat, India. TRAFFIC, New Delhi, India. 48pp
- Heyman W, Graham R, Kjerfve B, Johannes RE (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Marine Ecology progress Series 215: 275-282
- Holmberg J, Norman B, Arzoumanian Z (2008) Robust, comparable population metrics through collaborative photo-monitoring of whale sharks *Rhincodon typus*. Ecological Applications 18: 222-233
- Holmberg J, Norman B, Arzoumanian Z (2009) Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. Endangered Species Research 7: 39-53
- IUCN (2009) IUCN Red List of Threatened Species. Version 2009.1, International Union for the Conservation of Nature and Natural Resources. www.iucnredlist.org. last accessed 18.09.09
- Jonahson M, Harding S (2007) Occurrence of whale sharks (*Rhincodon typus*) in Madagascar. Fishery Research 84: 132-135
- Mahingika H, Potenski M (2009) Whale shark monitoring via observational surveys in Mafia Island, Tanzania. . In: Sixth Scientific Symposium of WIOMSA, Reunion
- Meekan MG, Bradshaw CJA, Press M, McLean C, Richards A, Quasnichka S, Taylor JA (2006) Population size and structure of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. Marine Ecology Progress Series 319: 275-285
- Nelson J, Eckert S (2007) Foraging ecology by whale sharks (*Rhincodon typus*) within Bahia de los Angeles, Baja California Norte, Mexico. Fishery Research 84: 47-64
- New A, Stansfield K, Smythe-Wright D, Smeed A, Evans A, Alderson A (2005) Physical and biochemical aspects of the flow across the Mascarene plateau in the Indian Ocean. Philosophical Transactions of the Royal Society A 363: 151-168
- Otis DL, Burnham KP, White GC (1978) Statistical inference for capture data on closed animal populations. Wildlife Monographs 62: 1-135
- Pollock KH, Marsh H, Lawler IR, Alldredge MW (2006) Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. Journal of Wildlife Management 70: 255-262
- Riley MJ, Hale MS, Harman A, Rees RG, 2010. Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives Archipelago. Aquatic Biology 8: 145-150
- Rowat D (1997) Seychelles whale shark tagging project - pilot project report. Phelsuma, Nature Protection Trust of Seychelles 5: 77-80
- Rowat D, Meekan MG, Engelhardt U, Pardigon B, Vely M (2006) Aggregation of juvenile whale shark (*Rhincodon typus*) in the Gulf of Tadjoura, off Djibouti. Environmental Biology of Fishes. 80: 465-472

- Rowat D, Gore M (2007) Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. *Fishery Research* 84: 32-40
- Rowat D, Speed CW, Meekan MG, Gore M, Bradshaw CJA (2009a) Population abundance and apparent survival estimates of the Seychelles whale shark aggregation. *Oryx*. 43: 591-598
- Rowat D, Gore M, Meekan MG, Lawler IR, Bradshaw CJA (2009b) Aerial survey as a tool to estimate whale shark abundance trends. *Journal of Experimental Marine Biology and Ecology* 368: 1-8
- Schmidt JV, Schmidt LV, Ozer F, Ernst RE, Feldheim KA, Ashley MV, Levine M (2009) Low genetic differentiation across three major ocean populations of the whale shark, *Rhincodon typus*. *PLoS One*. 4: e4988
- Schwarz CJ, Arnason AN (1966) A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*. 52: 860-873
- Smith A, (1828). Description of new, or imperfectly known objects of the animal kingdom, found in the south of Africa. *African Commercial Advertiser* 3pp
- Speed CW, Meekan MG, Bradshaw CJA (2007) Spot the match – wildlife photo-identification using information theory. *Frontiers in Zoology* 4: 1184-1182
- Theberge MM, Dearden P (2006) Detecting a decline in whale shark *Rhincodon typus* sightings in the Andaman Sea, Thailand, using ecotourist operator-collected data. *Oryx*. 40: 337-342
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*. 46: 120-13